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THE UNIVERSITY OF ALBERTA

PERMINERALIZED PLANTS FROM THE EOCENE, ALLENBY FORMATION OF SOUTHERN BRITISH COLUMBIA

by

© JAMES FREDERICK BASINGER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Permineralized Plants from the Eocene, Allenby Formation of Southern British Columbia", submitted by James Frederick Basinger in partial fulfilment of the requirements for the degree of Master of Science.

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Date July 30, 1976

ABSTRACT

Mass collections from the Ashnola locality, near Princeton, British Columbia, have revealed a far more extensive and diverse flora than previously recognized. Plant parts have been permineralized with silicates and are found in an outcrop of interbedded chert and coal. The age of the Ashnola locality is established as Middle Eocene on the basis of numerous K-Ar dates from associated strata and palynological data.

A comparison of the Ashnola locality with other permineralization localities establishes the Ashnola flora as one of the most diverse assemblages of well-preserved permineralized plants yet discovered in the early Tertiary. *Pinus arnoldii*, *P. similkameenensis*, and a semiaquatic dicotyledon, *Eorhiza arnoldii*, which have been described previously by Miller (1973) and Robison and Person (1973), are re-examined. The present study includes brief descriptions of three ferns including *Dennstaedtiopsis aerenchymata*, taxodioid reproductive and vegetative remains assignable to *Metasequoia*, pollen cones of the genus *Pinus*, and leaf remains of sabaloid palms. A report of diverse reproductive and vegetative angiospermous organs is also included. Of greatest interest are numerous flowers whose fine preservation allows assignment not only to the Rosaceae, but to specific tribes within the family. This is the earliest record of rosaceous floral anatomy and provides valuable information on evolution within the Rosaceae.

The Ashnola flora is similar to compression localities in the area in containing a combination of temperate and subtropical elements. Reasons for this mixing are proposed and the confusion that this assemblage has introduced into early attempts at age determinations is reviewed.

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CHAPTER 1

INTRODUCTION

Material from the Ashnola locality was mass collected during the summers of 1974 and 1975 and has yielded large quantities of permineralized megafossils. The locality is found on the east bank of the Similkameen River approximately 5 miles south of Princeton, southern British Columbia, and forms an outcrop of interbedded chert and coal that extends across the river to form a partial dike. The plants are permineralized with, and are found embedded in, the silicates which form the cherty layers. Although the age of the Allenby Formation, of which the Ashnola locality is a part, has been questioned in the past, recent evidence indicates a Middle Eocene age.

Compressed megafossils and dispersed palynomorphs are common in Tertiary sediments and provide information about external morphology and paleofloristics, but they can contribute little to our understanding of internal anatomy, organ development, or reproductive mechanisms of Tertiary plants. By contrast, permineralized plants showing internal structure can provide this latter information. Permineralization fossils are, however, quite uncommon in the Tertiary and, with the exception of permineralized wood, only a few specimens have been found at any one locality. It will be seen that the Ashnola locality contains the most diverse flora of well-preserved, permineralized megafossils yet discovered in the early Tertiary.

Only in the last 10 years has the potential of the Ashnola locality been recognized. Unlike most highly productive megafossil localities, the locality went unnoticed by amateur collectors, largely because the fossils are not immediately obvious on the chert surface and are virtually impossible to detect on a freshly broken and unweathered face. If not cut and treated with hydrofluoric acid to reveal the entombed plants, the blocks of chert are anything but aesthetically pleasing.

Arnold and Boneham were first to exploit the Ashnola locality and a palynological study was made by Boneham (1968). Material from their collection was made available to Miller (1973), who described Pinus arnoldii and Pinus similkameenensis, and to Robison and Person (1973), who described a semi-aquatic dicotyledon called Eorhiza arnoldii. These authors also reported the presence of two or three ferns including Dennstaedtiopsis aerenchymata Arnold and Daugherty (1964), dicot stems, an ascomycete fungus, fragments of one or more moss gametophytes, and a few seeds of unknown affinity. The diversity found during the present study has, however, far exceeded that previously recognized.

The primary objective of this thesis is to present an account of this diversity and to present detailed reports of some of the more conspicuous elements of the flora. Included in these reports are male cones of the Taxodiaceae and Pinaceae, fern rhizomes and petioles, and petioles and lamina of a sabaloid palm. Of greatest interest were numerous flowers whose preservation is fine enough to allow an assignment to not only the Rosaceae, but to specific tribes within the family. This is the earliest known record of rosaceous floral structure and has provided valuable information on floral evolution within the Rosaceae.

Paleoecology will be discussed in reference to both the florule of the Ashnola locality and to the flora of the Allenby Formation in general. Subtropical forms such as the sabaloid palms which are the first palms reported from the Allenby Formation, together with pines and other temperate forms show a complex mixing of northern (Arcto-Tertiary) and southern (Neotropical-Tertiary) elements of the flora of Eocene North America. Causes of this mixing will be explored and the confusion that the resulting assemblage introduced into early attempts at age determination of the Allenby Formation will be reviewed.

Tertiary Fossil Remains

Fossil remains of Tertiary vegetation occur primarily as compressed megafossils and dispersed palynomorphs. Although these fossils provide us with information on external morphology and paleofloristics, they reveal little of internal structure or reproductive mechanisms.

Our understanding of evolutionary relationships among plants is based primarily upon characteristics of reproductive structures and development and to a lesser degree on vegetative characteristics. Our modern schemes of classification are constructed by evaluating these characteristics.

Because the more delicate and somewhat ephemeral reproductive organs are seldom found in the compressed state, classifications based on fossil genera have been constructed primarily on vegetative features. As we know it is very difficult to accurately assign a taxonomic position to living genera unless both vegetative and reproductive organs are known. This difficulty is compounded for fossil plant remains because of the fragmentary, often incomplete nature of the fossil record and the fact that different plant structures for a given genus may evolve at different rates. Christophel emphasized this latter point when he stated (1973, p. 26):

> "... the similarity of a fossil leaf (or other plant organ) to an extant counterpart does not, indeed cannot, be taken as evidence that the entire extinct and extant organisms are identical (at the generic level). To do so denies the paleobotanically proven fact that different plant structures evolve at different rates in certain organisms and negates the possibility that the majority of the organs of a given plant may have evolved into generic uniqueness in a given number of million years while one organ remained unchanged."

An example of differing rates of evolution can be found in the Juglandaceae of the lower Tertiary, where leaves of the genera Juglans and Carya were found attached to very similar reproductive organs (Chaney, 1949b). Although these two genera were differentiated vegetatively by the Eocene, distinct reproductive morphology had not yet appeared. On the other hand pollen grains and fruits of Engelmannia are common in lower Tertiary sediments, but leaves of this genus have not been recognized from these same strata (Dilcher, (1973). It is apparent that reproductive organs of Engelmannia had evolved by the early Tertiary, but leaf structure had not yet changed to its present state.

The examples given show that this approach applies to both isolated reproductive and vegetative organs. However, since modern systems of classifications are principally derived from reproductive characters, conclusions of taxonomic affinity are more reliable if based on reproductive organs.

The adoption of this philosophy expressed by Christophel leads one to restrict the application of modern generic names to those fossil plants that are quite well known vegetatively and reproductively. Isolated organs are assigned to form- and organ-genera. This allows for the classification of isolated organs without creating the erroneous impression that a modern genus, with all of its characteristics, existed at some time in the past.

Workers such as Berry (1916, 1924), Knowlton (1902, 1922), Hollick (1930, 1936), and Bell (1949) had not accepted such a view and assigned modern generic names to vegetative remains, particularly those of leaves, on the basis of gross structural similarities. Among other misconceptions, this approach resulted in a belief that Cretaceous and lower Tertiary floras contained high percentages of apparently highly evolved angiosperms. Recent work by Wolfe (1969), Hickey (1973), and Dilcher (1973, 1974) has largely dispelled this belief, for they have been able to show that large numbers of plant megafossils were misidentified by the early workers. Although workers such as Dilcher, Wolfe, and Hickey have been able to eliminate many of the problems arising from the assignment of modern generic names to incompletely known fossil plants based on vegetative remains, there still exists the problem of properly interpreting these vegetative remains in the absence of evidence from reproductive structures. Even if artificial classification schemes based on leaf structure are constructed, the uncertainty of the position of the extinct genera in natural systems of classification remains, as long as little or nothing is known of their reproductive characteristics.

Unlike compressed megafossils, permineralized (petrified) plants are able to provide information about internal structure and reproductive morphology. Permineralized specimens often reveal many delicate vegetative and reproductive organs of both woody and herbaceous plants showing superb structural detail. This is due in part to conditions present at the time of deposition. The Ashnola chert, like the Rhynie chert, American coal balls, and the Deccan Intertrappean cherts, was probably deposited in a very still water environment (see Locality-Formation). This type of depositional environment would allow an accumulation of more delicate plant parts in addition to more resistant organs. The permineralization of the accumulated debris effectively protects the more delicate plant parts from destruction by compression. Thus, they not only accumulate intact, but are retained in a recognizable state after fossilization. Only in permineralized plants are detailed anatomical studies possible. The gradual accumulation of plant organs also permits the preservation of many developmental stages of those organs, which provides an opportunity for developmental studies.

The fact that so few Tertiary petrifaction localities are known makes work in this area of critical interest. Since nearly all knowledge of Tertiary vegetation has been derived from compressed megafossils, exceedingly little is known of reproductive characteristics and the internal structure of these plants. The Ashnola chert has great potential in this area because of the great diversity of petrified reproductive and vegetative structures. Unfortunately, the rarity of Tertiary permineralized plants, in addition to the lack of knowledge in comparative anatomy of living plants, makes the study of material such as the Ashnola chert very difficult. It is also difficult to make comparisons of permineralized and compressed organs. External morphology is not immediately available in the former, while anatomical detail is unavailable in the latter.

The compilation of information from other Tertiary localities containing petrified plants which follows emphasizes that permineralized plants in the Tertiary are exceedingly rare and that little is presently known about them. The fact that so little information has been obtained from Tertiary plants preserved as petrifactions places the Ashnola chert in a position of considerable importance.

Tertiary Permineralization Localities

Considering the great value of permineralized plants, it is very unfortunate that so few localities have been discovered in Tertiary starta. With the exception of petrified wood, which occurs frequently in the Tertiary as isolated fragments, rarely more than a few specimens are reported from a single locality.

Permineralized lignite or degraded peat, such as that described by Ting (1972) from the Paleocene of North Dakota, has been found, but preservation is less than ideal due to degradation prior to preservation. Ting described the preservation as "comparable to that of Carboniferous coal balls" and that it was "the first reported finding of such material in North America". Unfortunately, the silicified peat is not extensive, for the material occurred as a lens only 15 cm. thick and 1 m. long. This cannot be compared to the extent of the Ashnola locality, where over 3 tons of material have been recovered to date without effecting any appreciable change in the outcrop. It is also apparent, from photographs of the North Dakota material (Ting, 1972, p. 165), that superior preservation is found in the Ashnola chert. Preservation, however, is sufficiently good in Ting's material to identify roots, wood fragments, fern sporangia, and seeds.

An assemblage of structurally preserved roots from a permineralized soil was described by Wheeler (1972) as part of the Miocene Taper Hill Flora of Colorado. Apparently there was little else recognizable within the nodules.

One of the more interesting fossil localities is the nut beds of the London Clay, which have been thoroughly described by Ried and Chandler in 1933. The seeds and fruits of the London Clay flora, which make up the largest component of the assemblage, have been permineralized with iron pyrites and occur in marine sediments. Ried and Chandler explained the formation of the beds by the rafting of vegetation from rivers into the sea, where different types of organs would become waterlogged, sink, and become concentrated at various distances from shore. External morphology and gross structure are readily seen in these fossils, but there is a lack of vegetative material with which to associate them. This is a reversal of the kind of problem often found in compressions. There is also a lack of developmental stages present, for essentially all seeds and fruits found were mature.

Plant-containing nodules have been described from Japan by Stopes and Fujii (1911). The nodules are also found in marine sediments and may have been formed in a manner similar to that of the London Clay deposits, but contain a greater variety of plant organs than the London Clay beds. Discoveries from this locality include the gynoecium of a flower that was described by Stopes (1910) as possibly liliaceous. The Japanese material is limited both in quantity and in the quality of preservation.

The nut beds of the Eocene, Clarno Formation of Oregon may be classified as casts and molds rather than permineralized fossils. Scott (1954), however, found some degree of structure visible. These nut beds may have been formed by rafting as were the London Clay nut beds, but a basic difference is the formation of the Clarno nut beds in a lacustrine environment.

The chert beds of the Deccan Intertrappean Series of India are quite comparable to those of the Ashnola locality in both structure and age and, until the present study, contained the most extensive petrifaction floras known in the Tertiary. It is felt that a detailed description of the Indian material is required if floral comparisons with the Ashnola material are to be attempted.

The Deccan Intertrappean Series

The Deccan Intertrappean Series of India represents perhaps the best known of Tertiary permineralization floras. The Deccan Traps are an extensive series of volcanics that cover an area of more than 200,000 square miles with a maximum thickness of about 2100 meters (Rao, 1936). Thin sedimentary layers are found between successive lava flows of the Lower (about 450 meters) and Upper (about 150 meters) Traps and are called the Lower and Upper Intertrappean Series respectively (Blanford, 1867; Rao, 1936). The Middle Traps (about 1200 meters) are devoid of Intertrappeans.

The Intertrappeans were formed in hollows on the lava sheets and contain lacustrine or marsh deposits, and the nature of the fossil remains reflects this type of depositional environment. These sedimentary beds are not large, each having a lateral extent of no more than three to four miles and a thickness of ½ to 3 meters (Prakash, 1960; Lakhanpal, 1970b).

Early workers such as Malcolmson (1837), Hislop and Hunter (1855), and Oldham (1871) concluded that the Traps were of an early Tertiary age, basing their conclusions on fossil evidence. Although an Upper Cretaceous age was later proposed on the basis of stratigraphic correlation with associated Mesozoic strata (Medlicott and Blanford, 1879; Wadia, 1919; Holland, 1926), recent work has supported an early Tertiary (Eocene) age for the Lower Traps (Woodward, 1908; Sahni, 1934, 1941; Sahni and Rode, 1934, 1943; Rao, 1935; Crookshank _et al_, 1937; Rao and Rao, 1939; Prakash, 1960; Lakhanpal, 1970a).

The flora of the Upper Intertrappeans is less extensive and less well known than that of the Lower Intertrappeans. Rao (1936) believed that the differences between the floras of the Upper and Lower Intertrappeans and the extent of the lava flows comprising the Traps indicate a Miocene age for the Upper Intertrappeans.

The flora of the Deccan Intertrappeans is very rich and varied, with almost 200 species reported to date. It must be remembered, however, that the Traps are extensive beds and extend through considerable time as well as space. The large number of localities with a variety of species is, to a great degree, responsible for the diversity. In addition to elements of space and time, ecological factors have resulted in considerable differences among the individual florules, adding to the diversity of the composite flora. At Rajahmundry, plant remains are exclusively aquatic and consist basically of Chara and other algal forms indicative of estuarine conditions (Pia, Rao, and Rao, 1937a,b; Rao and Rao, 1939; Rao and Rao, 1940). Aquatics are also found at Sausar, but unlike Rajahmundry, the flora has the aspect of fresh water lakes or marshes. Included in the flora are charophytes and other algae (Sahni and Rao, 1943), Azolla (Sahni, 1941), and some other pteridophytes (Lakhanpal, 1970b). The richest of all known localities in the Deccan Intertrappeans is that of Mohgaon Kalan. This locality appears to represent an ancient marsh that contains, in addition to aquatics such as algae, bryophytes, and water-ferns, conifers, dicots, and monocots of which there is a predominance of palms. Comprehensive lists of species from Mohgaon Kalan, as well as from all other known localities in the Deccan Intertrappeans, can be found in Sahni (1931), Prakash (1960), Lakhanpal (1970b), and Rao and Achuthan (1971). These three localities, Rajahmundry, Sausar, and Mohgaon Kalan, have yielded an abundance of good material, but material from the numerous other localities rarely consists of more than a handful of specimens.

Considering both spacial and temporal differences, as well as differences in habitat and floral composition among localities, it does not seem reasonable to support the proposition of a single massive flora. Individual localities appear to have their own unique floras, and should be treated as such and not collectively (Lakhanpal, 1970b).

If identifications of specimens from the Intertrappeans are correct, then the fossil floras apparently had much the same aspect as do the modern floras of that region and of tropical South America (Prakash, 1960; Lakhanpal, 1970b). The presence of *Nipa* (Sahni and Rode, 1937; Chitaley, 1960), *Musa* (Jain, 1964a,b) and *Heliconiaites* (Trivedi and Verma, 1972) of the Musaceae, and certain palms indicates a tropical climate (Lakhanpal, 1970b). Petrified woods lack distinct seasonal growth rings as well. There are some more temperate forms such as *Sparganium* found in the fossil floras (Lakhanpal, 1970b), but their presence has not yet been explained.

At both the Rajamundry and Sausar localities are found basically aquatic forms such as algae; therefore, neither compares favorably to the Ashnola locality which is composed primarily of vascular plants which grew adjacent to the depositional area. The depositional environment of the Ashnola locality compares most favorably, then, to the Mohgaon Kalan locality. Mohgaon Kalan is also the only Intertrappean locality that can be considered comparable to the Ashnola locality in degree of diversity and quality of preservation. However, a direct comparison of plants found in the two localities is impossible, for the flora of Ashnola, as will be seen, is composed primarily of warm temperate to subtropical forms which show no similarity to the basically tropical elements of Mohgaon Kalan.

The Clarno Chert

The Clarno chert of Oregon is found in the Middle Eocene, Clarno Formation and is relatively similar in appearance to the Ashnola chert. There is some basis for believing that both the Clarno and Ashnola chert beds are in some way related (see Geology-Locality). The Clarno and Green River Formations have long been known to contain an abundance of silicified wood as well as fern stems (Arnold, 1945, 1952). Arnold and Daugherty (1963, 1964) were first to report on the Clarno chert, which was found below a lava sheet and above a 130-meter thick ash bed. The chert is light grey, a color imparted by quantities of ash within the matrix, and forms a bed less than one meter thick. As a result of their study, two ferns were described from the chert, *Acrostichum preaureum* (Arnold and Daugherty, 1963) and *Dennstaedtiopsis aerenchymata* (Arnold and Daugherty, 1964). These two reports also note the presence of *Equisetum*, twigs of herbaceous and woody dicotyledons, wood of *Ginkgo*, and numerous palynomorphs. *Equisetum clarnoi* was recently described from the locality by Brown (1975). The Clarno chert was the first petrifaction locality containing an abundance of well-preserved herbaceous plants to be found in the Tertiary of North America. As yet, however, the diversity of the flora has not been proven great.

Permineralized plants of the Tertiary have, due to their rarity, offered little to our understanding of Tertiary vegetation. This is unlike the Carboniferous, where much of our knowledge of Upper Paleozoic plant structure, both vegetative and reproductive, is based on the coal-ball floras. The value of the information derived from these Paleozoic petrifaction floras is quite apparent. It is expected, then, that the discovery and investigation of such floras in the Tertiary could likewise contribute a wealth of knowledge of Cenozoic plant structure and reproductive mechanisms.

The Ashnola Locality

The Ashnola locality is the first locality found in North America that offers an extensive survey of permineralized Tertiary plants. All other Tertiary permineralized beds located in North America are limited by the quality of preservation, the abundance of material, or the diversity of the flora. In these respects, the Ashnola chert is rivaled only by the cherts of the Deccan Intertrappean Series.

The Ashnola locality was first described by Boneham (1968), who reported the presence of pine cones and needles and rhizomes of *Dennstaedtiopsis aerenchymata* Arnold and Dautherty (1964). The pine cones and needles were described by Miller (1973) as *Pinus arnoldii* and *P. similkameenensis*, respectively. A semiaquatic dicotyledonous rhizome, *Eorhiza arnoldii*, was described at the same time by Robison and Person (1973). These same reports indicate the presence of woody stems of two or more dicots, ferns, bryophyte remains, unidentified seeds, and an ascomycete fungus. The diversity found in the present study is much greater than previously suspected. In both abundance of material and quality of preservation, the Ashnola locality is comparable to the best coal-ball localities of the Carboniferous, and it is possible that the Ashnola locality will provide an understanding of Tertiary fossil floras in a way that some coal-ball localities have helped in our understanding of Carboniferous floras.

2

CHAPTER 2

GEOGRAPHY and GEOLOGY

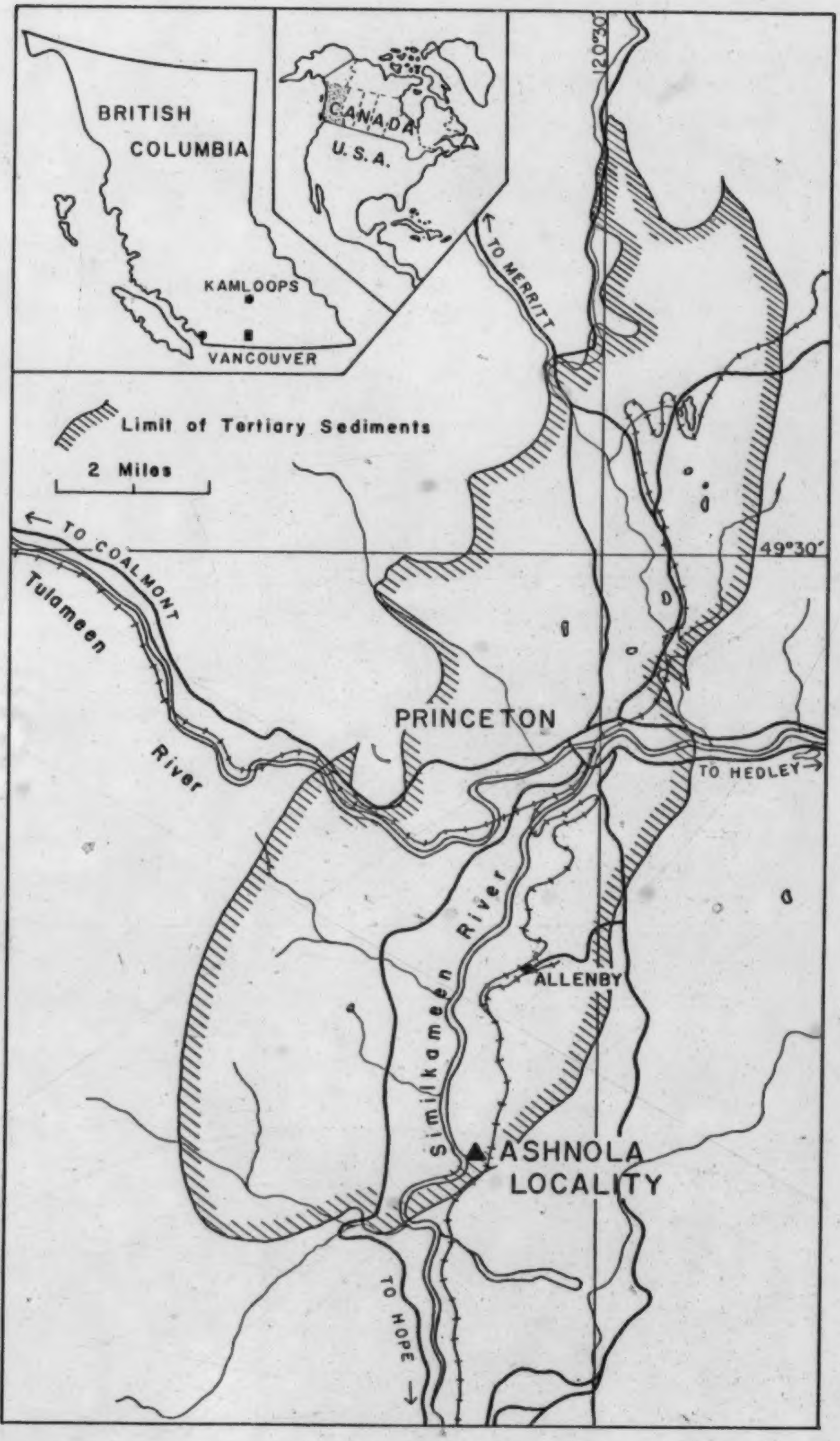
Geography

The Ashnola locality is found on the east bank of the Similkameen River approximately 5 miles S.S.W. of the town of Princeton, British Columbia. The locality is slightly more than 2 miles S.S.W. of the abandoned town of Allenby and almost directly across the river from the abandoned mining camp of Ashnola (Princeton Map Sheet 92 H/7 1:50,000 U.T.M. Grid Ref. 783 724). Boneham (1968) referred to this as locality "I" during his palynological studies, but it is here named the Ashnola locality (see Fig. 1).

The town of Princeton is found to be at the approximate center of a small, natural basin which contains a considerable thickness of sedimentary rocks (see Geology). These sediments were determined by Camsell (1907) to extend approximately 14 miles north to south and from 3½ to 5 miles east to west. The Ashnola locality is found near the southern limit of the sediments. The soft nature of the Tertiary deposits as opposed to the very resistant Triassic volcanics which surround and underlie the basin provides for an abrupt topographic change upon entering the Princeton basin. Dawson (1879, p. 49B) described this change as he entered the basin from the southwest:

> "These (Mesozoic volcanics) are now succeeded by softer igneous and sedimentary beds of the Tertiary, and the whole aspect of the country at the same time

Fig. 1. Map of the Princeton area showing the Ashnola locality in relation to the Tertiary sediments of the Princeton basin and local geographic features. (After Shaw, 1952)


BRITISH COLUMBIA
KAMLOOPS
VANCOUVER
CANADA
U.S.A.
120°30'
49°30'
Limit of Tertiary Sediments
2 Miles
TO MERRITT
TO COALMONT
Tulameen River
PRINCETON
TO HEDLEY
Similkameen River
ALLENBY
ASHNOLA LOCALITY
TO HOPE

> changes for the better. The valley widens, and the brook (Whipsaw Creek) cuts rapidly down to a lower level, running between high terraced banks with occasional cliffs of volcanic rocks."

There are no volcanic cliffs at the Ashnola locality, but here the Similkameen River does flow at the foot of a steep embankment on the eastern side of the broad, deep valley cut by the river. On the west bank, opposite the locality, is a flat and open field, now used for agricultural purposes, that probably represents earlier river channels and flood plain. The Ashnola chert is apparently more resistant than most other rocks in the area, for it forms a partial dike across the river while surrounding strata have long since been eroded by the water (see Fig. 2).

Although there is little glacial drift at the Ashnola locality, large quantities of the material blanket most of the area, and solid rock is usually only exposed by stream cuts. Camsell (1907) notes that this drift imparts "an appearance of fairly mature erosion, giving to the hills in the belt a rounded and graded outline", a characteristic that is a conspicuous feature of the Interior Plateau of British Columbia, onto which the Princeton basin abuts along its northern margin.

The Princeton basin is found between two forks of the Cascade Range and is contained on the west and south by the true Cascades (including the Hozameen and Hope Mountains), and on the east by the eastern Cascades or Okanagan Range. To the north, the country opens out into the Great Interior Plateau (Camsell, 1907).

Fig. 2. View of the Ashnola locality looking northwest from the east bank of the Similkameen River. The outcrop of interbedded chert and coal extends into the river to form a partial dike.

The elevation of the Ashnola locality is slightly more than 700 meters, which is about 100 meters above the townsite of Princeton. The nearby hills approach 1300 meters, and altitude gradually increases to the south, east, and west.

Geology

The first geological studies of south-central British Columbia were made by Bauerman in 1859-1861, although this work was not published until 1884. Bauerman recognized the presence of Tertiary deposits in a number of the natural basins of the area. Among these were the deposits of the Princeton area, or Vermilion Forks as it was known at that time.

A later study, although published before that of Bauerman, was completed by Dawson (1879). Unlike Bauerman, Dawson showed considerable interest in the Tertiary basins and has provided a detailed report on the geology of the Princeton area.

Camsell (1907, 1915) considerably extended the study begun by Bauerman and Dawson. Camsell attempted to give a history of the formation of the Princeton basin as well as a description of the present structure. Later studies were made by Rice (1947), Shaw (1952), and Hills (1962, 1965a,b).

The Tertiary deposits of the Princeton basin lie unconformably on the Triassic volcanics of the Nicola Group, named by Dawson in 1879. The Nicola Group is also found to underlie a number of other Tertiary basins in the area such as the Tulameen and Merritt basins (Dawson, 1879; Boneham, 1968). These Triassic basement rocks have suffered distortion and severe erosion, likely due to uplift during the Upper Cretaceous (Camsell, 1907; Shaw, 1952). Some sediments of a Lower Cretaceous age are present in the vicinity of the Princeton basin, but there appears to have been no deposition of sedimentary rocks in the area during the Upper Cretaceous.

Regional subsidence must have occurred during the early Tertiary to create the many basins of the area which now contain deposits of this age. This explanation accounts for the volcanism at the beginning of this period and for the great thickness of the deposits in a basin such as the Princeton, where there are possibly 2500 meters of beds. Other possible causes such as valley damming by lava flows cannot account for such a thickness of beds (Shaw, 1952) . The early Tertiary sediments have since been folded and faulted, with dips ranging from 10° to 45°. This is probably a result of uplift responsible for the creation of the Cascade Mountains during the late Tertiary.

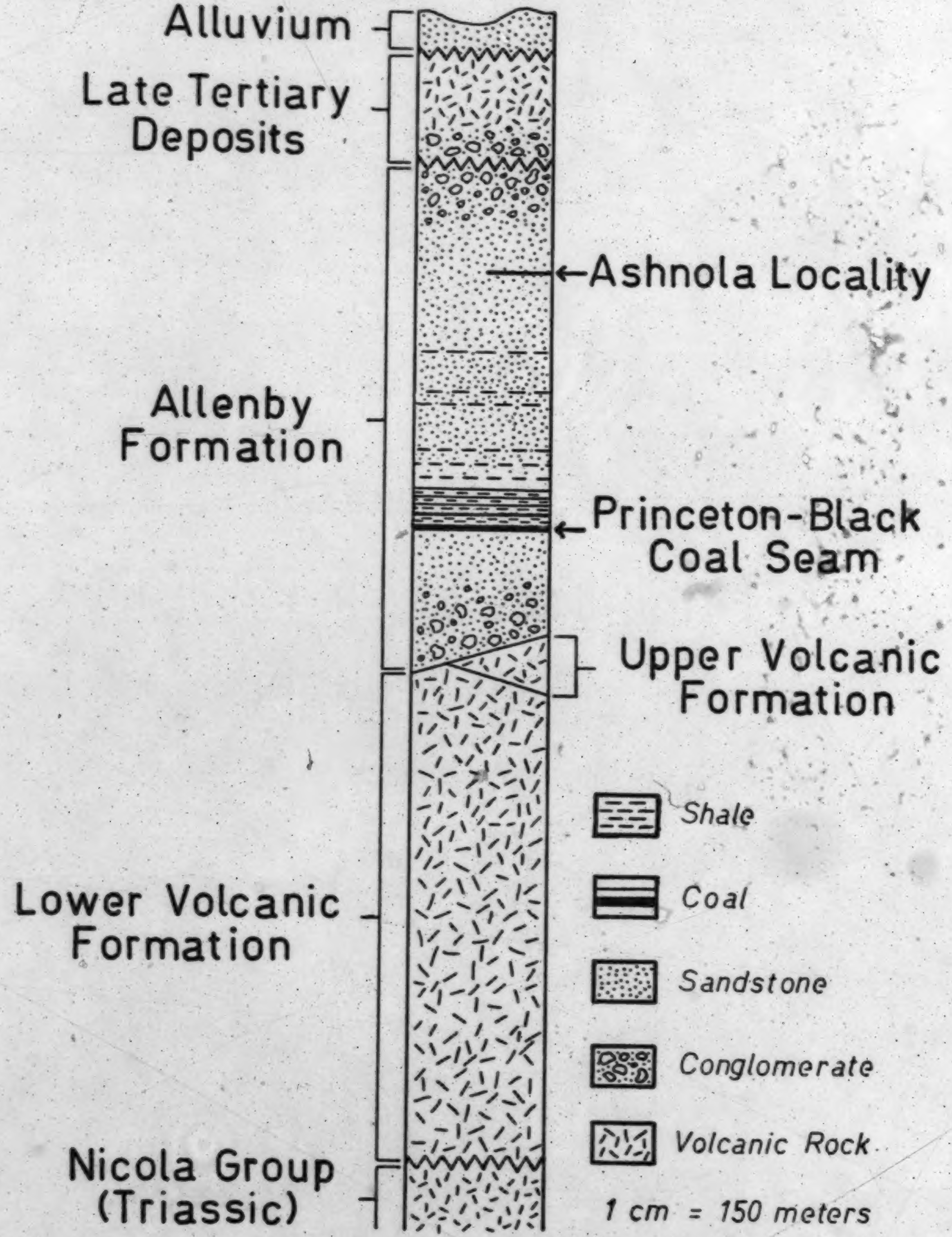
Both volcanic and sedimentary beds were recognized as part of the Tertiary deposits of the Princeton basin by Dawson (1879) and Camsell (1907). Rice (1947) described the Princeton lavas as forming the bulk of the Tertiary deposits and as existing both above and below the sedimentary beds. Shaw (1952) first gave a fairly detailed description of the deposits and recognized three formations within the Princeton basin. They were, in ascending order, the Lower

Volcanic Formation (1400 meters thick), the Allenby Formation (1100 meters thick), named after an outcrop near the town of Allenby, and the Upper Volcanic Formation (150 meters thick) (see Fig. 3).

The Tertiary sediments, the Allenby Formation, cover an area of approximately 40 square miles, extending about 14 miles north to south and 3½ to 5 miles east to west. The Ashnola locality, as noted in the previous chapter, lies near the southern limits of the Allenby Formation. Boneham (1968) was the first to study the Ashnola locality and determined its stratigraphic position as 550 meters above the Princeton-Black coal seam, or about 850 meters above the base of the Allenby Formation.

That the Ashnola locality is a part of the Allenby Formation, and not a part of more recent, unconformable sediments, has been established. The possibility of unconformities within the Allenby Formation has been considered by Rice (1947), Shaw (1952), Russell (1958), and Hills (1962, 1965a). This uncertainty was due to the discrepencies in proposed ages of the sediments based on identifications of megafossils. On the basis of evidence from structure, composition of the sediments, and palynology, however, these same authors considered such a situation unlikely. There are late Tertiary sediments in the basin, however. Mathews and Rouse (1963) made a study of these deposits and found them to be late Miocene or early Pliocene in age, nearly flatlying, and scattered over a wide area in southern

Fig. 3. Stratigraphic relationships of Tertiary deposits of the Princeton basin.


Alluvium
Late Tertiary Deposits
Allenby Formation
Lower Volcanic Formation
Nicola Group (Triassic)
←Ashnola Locality
←Princeton-Black Coal Seam
Upper Volcanic Formation
Shale
Coal
Sandstone
Conglomerate
Volcanic Rock
1 cm = 150 meters

British Columbia. Outcrops of these deposits, however, have not been recognized in the vicinity of the Ashnola locality.

Palynological studies by Boneham (1968) have shown that there was no significant difference between the Ashnola locality and other localities of the Allenby Formation that would indicate an unconformity. Of great importance is the discovery of an abundance of Pistillipollenites macgregorii Rouse at the Ashnola locality by Boneham (1968). This species has been reported from the Allenby Formation by Rouse (1962), Mathews and Rouse (1963), Hills (1962, 1965b), and Hills and Baadsgaard (1967), and is considered to be an index fossil for the Lower and Middle Eocene (Rouse and Srivastava, 1970).

A more detailed account of the stratigraphy of the Princeton basin will serve to clarify the position of the Ashnola locality relative to other beds of the Allenby Formation as well as to the numerous localities that have been sampled for radiometric dating.

Volcanic Formations of the Princeton Basin -

Rice (1947) described Tertiary volcanic deposits above and below sediments in the Princeton basin. Shaw (1952) named these the Upper and Lower Volcanic Formations. The Lower Volcanic Formation outcrops at the southern and western margins of the basin and is there found at its greatest thickness. These volcanics overlay principally the Triassic volcanics of the Nicola Group, and are overlain by the Allenby Formation in the northern and eastern parts of the basin. The Allenby Formation and the Lower Volcanic Formation appear to be conformable (Rice, 1947; Shaw, 1952; Hills, 1962, 1965b). The Lower Volcanics wedge out toward the north-east and are not found at the northern and eastern limits of the Tertiary deposits. In this area, however, are found rocks of the Upper Volcanic Formation. This formation finds its greatest thickness in the east and apparently wedges out toward the center of the basin.

Hills (1962) reinvestigated the Princeton volcanics and found that both Rice (1947) and Shaw (1952) were in error in placing the Upper Volcanic Formation above the Allenby Formation. Hills (1962, 1965b) has established that many of the outcropping volcanics are actually underlying the Allenby Formation and are possibly a part of the Lower Volcanics. Hills also refers to a number of smaller volcanic outcrops that were apparently included in the Upper Volcanic Formation, but which may be late Tertiary in age. Thus, the Upper Volcanic Formation of Shaw (1952) does not exist as such.

Late Tertiary Volcanic Deposits -

Although not directly involving the Ashnola locality, late Tertiary deposits are found in parts of the basin and may be responsible to some degree for misinterpretations of the age of the Allenby Formation (see Discussion). These once extensive deposits have also shielded the early Tertiary sediments from severe erosion during the Pleistocene.

Late Tertiary deposits are found in the northern and eastern parts of the basin and were called the post-Oligocene of Plateau Volcanics by Camsell (1907), but were apparently lumped together with older volcanic rocks to become the Upper Volcanic Formation by Shaw (1952). Hills (1962) recognized late Tertiary deposits when he reviewed the status of the Upper Volcanic Formation, but did not provide a description of them. Mathews and Rouse (1963) found these flat-lying deposits scattered over much of southern British Columbia and believe, as Camsell did, that they represent lavas that once covered the entire area. Three K-Ar dates obtained from these rocks (Mathews and Rouse, 1963) indicate a late Miocene or early Pliocene age.

Camsell (1907) proposed that these once extensive lavas protected the underlying rocks from serious erosion during the Pleistocene Glaciation. They were, however, nearly completely destroyed themselves and now often appear as caps on the tops of the higher hills, where they form outcrops too small to map. The result, after glaciation, is a much greater thickness of the decomposed rocks of the Allenby Formation than would have been possible without such protection.

Mathews and Rouse (1963) also found occasional sedimentary beds within or conformably beneath the volcanic rocks. These authors feel that a number of plant fossils from these beds were collected by early workers and included in a larger collection from the early Tertiary, Allenby Formation. This error may have been responsible, in part, for the late Tertiary age assignment early workers gave to the Allenby Formation.

Allenby Formation -

Sediments of the Allenby Formation were first named and described in detail by Shaw, who states (1952, p.8):

> "The Allenby Formation consists predominantly of massive, crossbedded granule- and pebble-conglomerate, sandstone, and massive and thinly bedded shale, with inter calated beds of coal, carbonaceous siltstone and shale, and bentonite. All size gradations between conglomerate and siltstone are represented, but granule-conglomerate and coarse sandstone seem to predominate."

Shaw (1952) noted that the coarser conglomerates were confined to the lowermost strata, below the major coal zones, although less coarse conglomerates can be found throughout the Allenby Formation. These lowermost conglomerates were found by Hills (1965a) to contain high percentages of volcanic detritus of a local origin. Hills also noted some volcanic flows in this zone.

The composition of sediments was recognized by Rice (1947) and Shaw (1952) as being primarily granitic in origin, and Shaw (1952, p. 8) states:

> "The volcanic content has undoubtedly been provided by the nearby large areas of the dominantly volcanic Nicola group and Cretaceous volcanic rocks that now occupy lesser areas."

From a more detailed study of the mineral composition of the Allenby Formation as well as of the surrounding volcanics, Hills (1965a) determined the provenance of the Allenby sediments to be the Osprey Lake Intrusion which lies to the north of the Princeton deposits and actually contacts the Allenby Formation on the northern margin. Hills (1965a) also found evidence for a paleocurrent flow from the north or northwest.

The existence of unconformities within the sediments of the Princeton basin was considered unlikely by Rice (1947), Shaw (1952), Russell (1958), and Hills (1962, 1965a). However, stratigraphic zonation, based on the nature of the sediments of the Allenby Formation, was indicated by Shaw (1952) and Hills (1962, 1965a, b). The lowermost sediments are primarily conglomerates, and finer grain sediments are more dominant in the bulk of the upper sediments, although there is another zone of conglomerates in the uppermost strata.

Coal has been mined from exposures near the Princeton townsite since the early part of this century. Although several seams have been exploited, the Princeton-Black Seam has been found to be the thickest and most extensive (Rice, 1947; Shaw, 1952). The mapping of this coal seam as well as the drilling of boreholes in search of coal have proved very valuable stratigraphically. The Princeton-Black Seam is the lowest occurrence of mineable coal in the stratigraphic sequence and has been used by Hills (1962, 1965b) to divide the Allenby Formation into an upper and a lower unit. The sediments below the Princeton-Black Seam are over 300 meters thick and consist basically of coarser conglomerates and sandstones. Above the Princeton-Black Seam are over 600 meters of basically shaley strata. Hills (1965b) notes that sandstone lenses increase in frequency and thickness upward in this upper unit. Since the Princeton-Black Seam is easily recognized and its extent fairly well known, localities within the Allenby Formation are often assigned a stratigraphic position relative to the Princeton-Black Seam.

The Ashnola locality was found to be about 550 meters above the Princeton-Black Seam and 850 meters above the base of the Allenby Formation by Boneham (1968). Although the locality is near the top of the Allenby Formation, there are no conglomerates associated with it. A dense, black shale lies on top of the Ashnola beds, and a sandy shale is found beneath. Most associated strata have become covered by slumping, but those that are visible are comprised basically of sandstone. There is a lack of mineable coal in the Ashnola area as well as in the northern and eastern parts of the basin, all of which represent the uppermost strata of the Allenby Formation. The fact that such an extensive coal deposit at the Ashnola locality exists in a zone generally devoid of sizable coal seams would indicate that the Ashnola locality represents a local phenomenon and such deposition was not widespread.

Statigraphic zonation has also been recognized within the Allenby Formation by Hills (1965b) and Boneham (1968) on the basis of varying abundance of pollen and spore types. Although species vary in abundance, there are no abrupt changes in floral composition that would indicate an unconformity. Hills (1965b) lists a lower Bisaccate Zone (60 meters thick), an Azolla primaeva Zone (250 meters thick), the Princeton-Black Coal Zone (40 meters thick), and a Pistillipollenites macgregorii Zone which can be subdivided into an upper, bisaccate (600 ± meters thick), and a lower, Taxodium (60 meters thick) dominance subzone. Boneham (1968) basically disagrees with Hills' interpretation, but supports the idea of zonation within the Allenby Formation. It should be noted that Hills based his work on collections made primarily within 60 meters above and 300 meters below the Princeton-Black Seam. Boneham, on the other hand, primarily studied samples taken above the Princeton-Black Coal Zone. The only zone in which both Hills' and Boneham's studies have overlapped is in the Taxodium dominance subzone. Of this subzone Boneham states (1968, p. 33):

> "Apparently the only stratigraphic zone Hills and I agree upon is his Taxodium dominance subzone."

Boneham goes on to say that he could not substantiate the presence of Hills' lower zones due to the lack of representative sampling. It appears that Hills may have overinterpreted results from his single sample in the upper zone of the Princeton basin and his determination of zonation in the Tulameen (Coalmont) basin. However, consideration of the findings of both Hills and Boneham should give a reasonably accurate appraisal of zonation in the Princeton basin.

The Ashnola locality is well into Hills' Pistillipollenites macgregorii, bisaccate dominance subzone. Although

Boneham rejects the existence of this subzone on the basis of a general lack of *P. macgregorii* and bisaccate grains, *P. macgregorii* is exceedingly abundant at the Ashnola locality (Boneham, 1968) and remains of *Pinus* form a large component of the locality's megafossil flora. It is likely that microecological factors were causing variability which makes Hills' findings and the flora of the Ashnola locality apparently incompatable with Boneham's results. The differences in composition are not sufficient to suggest an unconformity between the Ashnola locality and other localities in the basin.

The Ashnola Locality

Age -

Direct evidence for the age of the Ashnola chert was presented by Boneham (1968) in the form of *Pistillipollenites macgregorii* Rouse, a palynomorph characteristic of the Middle Eocene (Rouse and Srivastava, 1970). Although no radiometric dates have been determined for the outcrop, many dates, indicating a Middle Eocene age, have been recorded for other deposits within the Allenby Formation as well as for localities within the Upper and Lower Volcanic Formations and volcanics from other basins in southern British Columbia (see Table 1). Since the Ashnola locality has been established as a part of the Allenby Formation, and there have been no unconformities found within the Allenby Formation or between the volcanic and sedimentary deposits of the basin, these radiometric dates will be considered as representative of the age of the Ashnola chert.

Early workers believed, although frequently with reservation, that the deposits of the Princeton basin, as well as those of other basins in the area, were of late Tertiary age (G.M. Dawson, 1879; J.W. Dawson, 1879, 1890; Scudder, 1879, 1895; Camsell, 1907; Rice, 1947; Shaw, 1952) (See Boneham, 1968).

Evidence for an Eocene age was first presented by Russell (1935) and Gazin (1953) in the form of Tillodont mammal remains, but the fragmentary nature of these fossils did not permit a conclusive age determination.

Both palynological and radiometric evidence became available during the 1960's and established a Middle Eocene age for the Princeton deposits.

Some degree of comparability among the microfloras of the Allenby, Burrard, Kitsilano, McIntosh, Green River, and Fort Union Formations were recorded by Rouse and Mathews (1961), Rouse (1962), and Hills (1965b). Rouse (1962) notes that all except the Fort Union Formation, which is Paleocene, are regarded as Middle Eocene.

Pistillipollenites macgregorii Rouse (1962) , which appears to be characteristic of the Middle Eocene (Rouse and Srivastata, 1970), has been reported from the Allenby Formation by Rouse (1962), Mathews and Rouse (1963), Hills (1962, 1965b), Hills and Baadsgaard (1967), and Boneham (1968). As noted previously, Boneham found this species in abundance at the Ashnola locality.

Potassium-Argon (K-Ar) dates were recorded by Rouse and Mathews (1961), Mathews (1963), Hills (1965b), and Hills and Baadsgaard (1967). The results of these reports are found in Table 1. Those determinations of Hills and Baadsgaard (1967) were published from Hills' thesis (1965). Where results from the two publications differ, the dates recorded by Hills and Baadsgaard (1967) are used. A few of the samples of Hills (1965b) and Hills and Baadsgaard (1967) have yielded ages which are either far greater or, in one case, much less than the mean. This is attributed to contamination by older rocks in the former, and to the use of glass shards, which do not appear to retain Argon well, in the latter.

The Sunday Creek and Sunday Summit localities are found about 20 miles south of the town of Princeton, and are believed to be in the uppermost part of the Lower Volcanic Formation, or at the base of the Allenby Formation where the sediments are interbedded with volcanics (Rice, 1947; Hills and Baadsgaard, 1967). All localities other than the Sunday Creek, Sunday Summit, Princeton, and Allenby localities, are found in other Tertiary deposits such as those of the Kamloops group (McAbee, Quilchena, Tranquille, Battle Bluff, Savona Mountain), Tulameen or Coalmont basin (Collins Gulch), and Smithers area (Driftwood Creek).

The large number of radiometric dates from a wide range of rock types and localities show excellent agreement and leave little doubt as to the true age of the Tertiary deposits. A mean value for the age of the Princeton deposits is 49 m.y., which places the Allenby Formation at Middle Eocene.

Correlation of Tertiary Deposits of Southern British Columbia -

The close approximation of the age of the Allenby Formation with the ages of other Tertiary deposits in southern British Columbia supports the theories of earlier investigators such as Camsell (1907), Penhallow (1907), and Rice (1947) that the Kamloops group and Princeton group are the same age.

Palynological data is also in agreement with such correlation. Palynomorphs are generally more readily available than megafossils and are often more useful in stratigraphic correlation. Rouse (in Rouse and Mathews, 1961) used both mega- and microfossils and found that the Princeton, Tranquille and Rock Creek beds were synchronous. Hills (1965b) apparently was able to find some correlation among all Tertiary beds that he sampled, from Princeton to as far north as Smithers.

Although these Tertiary deposits are found in isolated areas over much of south-central British Columbia and are of an equal age, it is unlikely that they were at one time continuous over the entire area. Some of the beds of the Coldwater and Kamloops groups appear to have been more extensive at one time, but those of the Princeton basin were probably never much more extensive than they are at

Table 1. Potassium-Argon dates of Lower Tertiary strata from southern British Columbia. All radiometric analyses were made by H. Baadsgaard, Dept. of Geology, Univ. of Alberta.

[1] R&M - Rouse and Mathews (1961)
M - Mathews (1963)(from Hills, 1965b)
H&B - Hills and Baadsgaard (1967)

Author[1]	Material	Locality	Date (m.y.)
R&M	Biotite	Princeton	48
R&M	Biotite	Tranquille	49
R&M	Biotite	Savona Mountain	45
R&M	Biotite	Rock Creek	49
M	Biotite	Kettle River	48
M	Biotite		46
M	Biotite		53
M	Biotite		48
M	Biotite		
H&B	Andesine	Sunday Summit	50
H&B	Oxyhornblende	Sunday Summit	48
H&B	Oxyhornblende	Sunday Summit	52
H&B	Biotite	McAbee	50
H&B	Andesine	McAbee	48
H&B	Sanidine	Quilchena	79
H&B	Glass Shards	Quilchena	22
H&B	Biotite	Allenby	50
H&B	Andesine	Allenby	49
H&B	Sanidine	Sunday Creek	47
H&B	Sanidine	Sunday Creek	50
H&B	Andesine	McAbee	51
H&B	Biotite	McAbee	57, 56
H&B	Sanidine	McAbee	67, 56
H&B	Oligoclase	Battle Bluff	51
H&B	Sanidine	Battle Bluff	50
H&B	Biotite	Battle Bluff	50
H&B	Biotite	Battle Bluff	48
H&B	Biotite	Collins Gulch	47
H&B	Sanidine	Driftwood Creek	126

the present (Hills, 1965b). The orogenic movements which initiated deposition in the early Tertiary apparently had the effect of creating numerous, isolated basins over a wide area.

Structure -

As noted earlier, the Ashnola locality forms a 10 meter thick outcrop of interbedded chert and coal that is exposed on the east bank of the Similkameen River and extends into the river to form a partial dike. Boneham (1968) determined the strike to be N 27°E and the dip, 34°N. The beds outcrop for a short distance up the bank and it was noticed that they are folded rather sharply some 12 meters above the water's edge.

Boneham measured each layer of chert and coal (see Fig. 2) and sampled each for palynological analysis. The validity of his numbering individual layers is here questioned, for the thickness of layers is highly variable. Many chert or coal layers are found to anastomose and the intervening layer is terminated at that point. There are, however, several exceptionally thick layers of chert and coal that were identifiable throughout their entire exposure. With these layers as markers, it was possible to divide the outcrop into 9 intervals, each ½-1½ meters thick, and containing a number of layers of chert and coal. Each of the 9 intervals is separated from others by a broad and continuous layer of coal. These 9 units are relatively easily recognizable throughout the outcrop, while numbers applied to individual layers will vary with position on the outcrop. I believe that this system of numbering better reflects intervals of chert formation and gives a more accurate description of layering of the chert and coal.

Formation -

The outcrop extends into the Similkameen River for somewhat less than half the stream width and then disappears into the river bed. On the opposite side of the river is flat, bottom land which presumably represents former river channels and flood plain. There is no trace of outcropping rock on the west bank. The chert beds apparently do not extend far beneath the river, for Boneham (1968) notes that there is no trace of chert in the well log of Blakemore Borehold #1, which was sunk almost directly across the river from the Ashnola locality. This led Boneham to believe that the beds were very restricted in lateral extent and that the bog in which the deposits accumulated was likewise small in area.

Boneham (1968, p. 37) has reviewed possible theories for the origin of chert deposits and has lumped them into two groups:

> "One group claims that the chert is contemporaneously deposited with other sediments. The other group maintains that chert is a postdepositional replacement of the host rock."

An initial inspection of the chert of the Ashnola locality disposes of the latter group, for there are plant remains preserved in it and thus could not be a result of postdepositional replacement.

A review of similar occurrences of plant-bearing cherts reveals that they have requirements in common for their formation. There must be a source of silicates, which is generally believed to be hot, mineral springs or geysers often associated with volcanic activity. The siliceous waters must be contained in a relatively quiet body of water and be precipitated to form a silica gel covering the bottom of the bog or marsh. Precipitation could be accomplished by excessive evaporation which would create a supersaturated condition (Arnold and Daugherty, 1963), or by a change in pH. Correns (1950) has shown that a change in pH from 9 to 5 will result in the precipitation of 2/3 of dissolved silicates from a concentrated solution. The silicates infiltrate the top layers of debris and mud at the bottom of the marsh and, with time and the expulsion of water, forms chert. Although silicified woods and other resistant plant organs can be found with some frequency in the fossil record, silicified herbaceous forms and more delicate organs are uncommon and almost restricted to beds formed in the above manner.

The rhythmic deposition of chert and coal as found at the Ashnola locality is a very rare occurrence, with the only other known instance being in the Devonian during the formation of the Rhynie chert of Scotland. Kidston and Lang (1917, p. 764) have proposed the following explanation for the formation of the Rhynie beds:

> "The whole history of the formation of the Rhynie Chert zone, at least of that portion from which our specimens were taken can be clearly read. ... By the decay of the underground parts of Rhynia and the falling down of withered stems (for this plant had no leaves) a bed of peat was gradually formed varying from an inch to a foot in thickness. The peat was then flooded and a layer of sand deposited on its surface. Again the Rhynia covered the surface, and this process of the formation of beds of peat, with the deposition of thin layers of sand, went on till a total thickness of 8 feet had accumulated.
>
> After the formation of 8 feet of alternating peat and sand local physical conditions must have altered, for water with silica in solution, possibly discharged from fumaroles and geysers, poured over the peat bed and sealed it up."

Of this type of deposition Taliaferro (1933, p. 50) states:

> "The cause of the rhythmic banding of cherts and shales has been discussed many times and the only two hypotheses which have survived the test of critical examination are those of coloidal segregation and periodic supersaturation."

Boneham (1968, p. 38) elaborates and applies this to the Ashnola locality:

> "Taliaferro goes on to explain what he means by colloidal segregation. Essentially this can only happen in sea water since the colloidal particles of silica must be electrically charged by the dissolved salts present in sea water before these silica particles will clump in large enough aggregates to precipitate. There is no evidence that sea water was present in the Princeton Basin during Allenby time. Innundation of the swamp or peat bog by hot water rich in silicic acid from nearby volcanic sources seems to be the most likely origin of the silica. This water was probably hot enough to kill the vegetation of the bog. As the hot water mixed with the acidic water of the bog some of the silica precipitated. When the water cooled, it became supersaturated with silica and more of it precipitated. With the gradual cooling of the water, plants were able to establish themselves and so form another layer of peat on top of the chert layer. There are igneous rocks below the tuffs within the Allenby

> Formation. Volcanic activity must have been prevalent during Allenby time, so there may have been hot springs in the Princeton Basin."

The cherts of the Eocene, Clarno Formation of Oregon may be comparable to the Ashnola cherts also. Although not found rhythmically interbedded with coal, the Clarno chert appears to represent the soil of an ancient marsh in which permineralization was the result of the precipitation of silicate from mineral-rich hot springs (Arnold and Daugherty, (1963). Arnold and Daugherty (1963, p. 216) proposed that:

> "The high evaporation rate coupled with the impeded outflow of the water in the marsh resulted in a build-up of silica in the mucklike soil, leading to development of silica gel. ... Solidification of the mineral-saturated soil and plant parts was the final stage of the process of fossilization which was brought about by the weight of a sheet of lava which finally covered the marsh. This resulted in expulsion of enough water to precipitate and harden the siliceous residue into chert, and at the same time effectively protect the deposit from erosion."

There may be some relationship between the Clarno and Ashnola cherts. Their general appearance is similar, although the Clarno chert has a high ash content which imparts a greyish color. Both localities are roughly the same age and are found in a similar geographical position, and may have been formed as a result of the same uplift and subsidence. It is unlikely that such rare occurrences as these chert beds would occur coincidentally in such close proximity in space as well as time. In addition, an important element in the floras of both the Clarno and Ashnola cherts is Dennstaedtiopsis aerenchymata Arnold and

Daugherty (1964), and it is possible that further research will reveal more similarities in floral composition.

The presence of thick beds of ash below and lava flows above the Clarno chert (Arnold and Daugherty, 1963) indicates a brief development of a flora during a fairly unstable period of volcanism. In this way, the Clarno chert appears most similar to the Deccan Intertrappean Series of India. The Intertrappeans are thin sedimentary layers "trapped" between sheets of lava. It is possible that the Intertrappeans were formed in much the same way as Arnold and Daugherty (1963) described for the Clarno chert.

Boneham's (1968) conclusions as to the formation of the Ashnola chert layers coincide generally with the observations presented here. The Eocene marsh of the Ashnola locality must have suffered periodic inundation with mineral-rich water. The lignite layers of Ashnola are apparently relatively pure and without silicate, so Arnold and Daugherty's (1963) proposal for a continual influx of minerals and a gradual accumulation of silicates in the muck of the ancient, Clarno marsh is not applicable to the Ashnola locality.

The Ashnola marsh was apparently spring fed and of low kinetic energy, for there are apparently no inorganic sediments in any of the chert or coal layers save one chert layer. This is unlike the Rhynie locality where Kidston and Lang (1917) report quantities of sand being deposited on top of successive layers of peat.

In some of the chert layers at Ashnola there is preserved a considerable thickness of well-preserved plant material. This may indicate a rapid accumulation of debris, a slow rate of decomposition, or both. A slow rate of decomposition would likely mean acidic conditions in the marsh and support Boneham's proposal for the precipitation of a silica gel through the mixing of mineral water with the water of an acid bog. The rapidity with which permineralization took place is evident in the high degree of preservation of even the most delicate tissues.

Only the Ashnola and Rhynie localities show rhythmic bedding of chert and coal, but a floral comparison of the two is impossible due to the vast difference in age. This type of formation allows for considerable accumulation of well-preserved material that contributes to a diversity unmatched in the Clarno and Intertrappean beds where only a single layer of chert is found at any one locality. The various layers of chert record changes in dominance, with the abundance of some forms varying greatly. This allows many plants to be studied more thoroughly than otherwise may have been possible if only one layer were available for study. It is also possible that seasonal differences reflected by the included plant parts may be found among the layers of chert. Such an assumption is supported by the observation of well developed growth rings in the twigs and wood fragments of woody dicots and conifers. As yet, the Ashnola locality has, in the Tertiary, proved to be unique in the abundance of material, the diversity of the flora, and the quality of preservation. In these respects, it is possible to say that the Ashnola locality is comparable to the best coal-ball localities of the Carboniferous.

Other Chert Beds in the Princeton Area -

The question arises as to the possibility of finding other chert beds in the Princeton basin, or perhaps in neighboring basins, since hot springs such as those believed responsible for the Ashnola chert may have been common in the area. That other chert beds occur in the Allenby Formation was noted by G.M. Dawson in 1879. Having no knowledge of the Ashnola chert, Dawson discovered fossiliferous chert at Vermilion Bluff, located on the Tulameen River about 3 miles west of the town of Princeton. The beds of this cliff are of a red to yellow hue which has been imparted by the combustion of a lignite seam, but the siliceous beds have resisted serious metamorphism. Dawson (1879, p. 131B) describes the cliff as follows:

> "On a closer examination of this section, however, it appears that the beds have originally differed in character from those usually found, and it becomes apparent that they have been laid down in the bed of a lake, into which very copious mineral springs have issued. The deposit of the springs has been chiefly siliceous, but there is much calcareous matter, and the water probably also contained iron, and other substances, all of which are now mingled with greater or less quantities or ordinary sediment. ...
>
> The rocks as they now appear consist broadly of sandstones, shaly argillites and siliceous layers, with some siliceous limestones toward the base of the section, in thin beds. The beds more directly resulting

> from the siliceous deposit of the springs are very varied in character. Black chert-like layers occur, but generally do not continue far horizontally. Other beds, similar in texture, are mottled with red, due to the oxidation of iron, and traversed by tube-like white or grey markings, which on close inspection are seen to be silicified grass stems, which have been included in the mass. One of these materials, microscopically examined proved to consist of dull amorphous silica through which cloudy flecks were scattered, and occasional larger opaque patches, coloured with iron oxide. The base also held minute crystals of calcite, irregularly distributed, on obtuse rhombohedrons, perfectly formed, and almost resembling cubes. The mass must have been deposited originally in a gelatinous state, about the stems of milky chalcedony, turning to crystalline quartz toward the center of each. The stems have in great part decayed away before the final consolidation of the mass, and have collapsed irregularly in the tubes, though still showing the structure of cellular tissues and spiral vessels under the microscope. In other layers, a grey porous material is not uncommon, and in many cases appears to be almost entirely made up of silicified vegetable fragments, of which the forms can scarcely be defined."

The chert of this locality has not been studied in any subsequent investigation of the Princeton basin, including the present one. It is my belief that a study of this chert may prove highly rewarding. Dawson's locality and the Ashnola locality show that proper conditions for chert formation were present in the Princeton basin at Allenby time, and it is quite possible that other localities may be found.

CHAPTER 3

MATERIALS and METHODS

Materials

Chert blocks were mass collected from the Ashnola locality in July of 1974 by W.N. Stewart, G.W. Rothwell, and the author and in August of 1975 by W.N. Stewart, G.W. Rothwell, R.L. Dennis, and M.S. Brosier. Prior to these collections, small amounts of material were taken from the locality by C.A. Arnold and R.F. Boneham in the early 1960's and by W.N. Stewart, G.W. Rothwell, and M.S. Brosier during an exploratory trip in May of 1974. Material collected by Arnold and Boneham was later made available to C.N. Miller (1973) and C.R. Robison and C.P. Person (1973). All material from the May, 1974 and July, 1975 collections has been deposited in the University of Alberta Paleobotanical Collection. The bulk of the material from the collection of August, 1975 was taken to Ohio University by G.W. Rothwell, with a lesser amount brought to the University of Alberta.

The structure and extent of the locality has been discussed in detail in the previous chapter. The outcrop consists of approximately 10 meters of interbedded chert and coal (Fig. 4). Over 30 layers of chert have been recognized by Boneham (1968), but they have been grouped into 9 units, numbered from the bottom to the top, in the present study. For most of the blocks, no attempt was made to determine and record their precise origin with the outcrop.

They were pried from the outcrop or picked up at its base and for about 100 meters downstream where they had been transported subsequent to weathering free. Collections were made, however, from each of the 9 units in order to determine whether or not floral zonation existed within the outcrop.

Unweathered blocks of chert vary from light grey to black in color. Weathered faces assume a grey to buff color with plant material visible on the surface (Fig. 5). It was suspected, and later confirmed during preparations of the blocks, that those lightest in color did not contain much of the original organic residues and had to be thin-sectioned for study. The opaque, black blocks, on the other hand, contained considerable organic material and were easily peeled (see Methods). Another supposition that proved correct was that these lighter blocks contained plant parts that were on the whole less well preserved than did the dark blocks, which is probably due to the greater length of time required for permineralization as indicated by the loss of organic matter. For these reasons, efforts were concentrated on the collection of the darkest chert. Care was taken, however, to obtain representative samples of all types of chert.

The texture of the rock was also found useful in the sorting of material in the field. Rich blocks with good preservation tended to occur in somewhat irregular shapes and freshly broken faces were glossy black. Pieces containing

Fig. 4. Closeup of the outcrop showing layers of blocky chert interbedded with coal.

Fig. 5. A block of Ashnola chert with plants evident on the surface (dark, circular markings).

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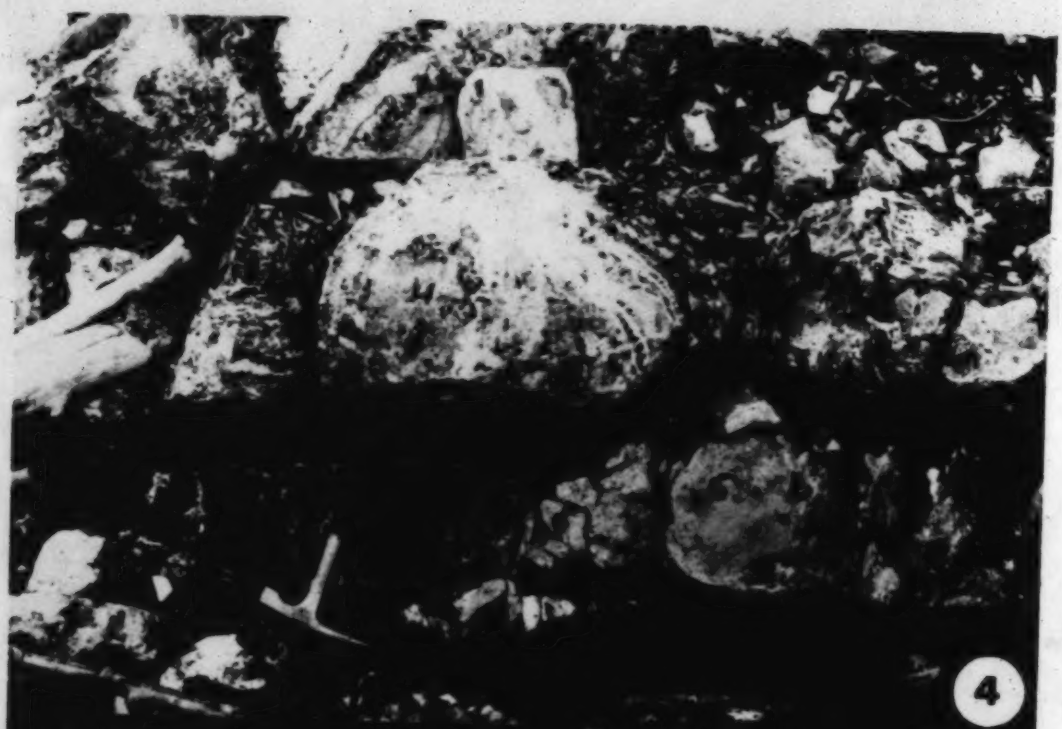

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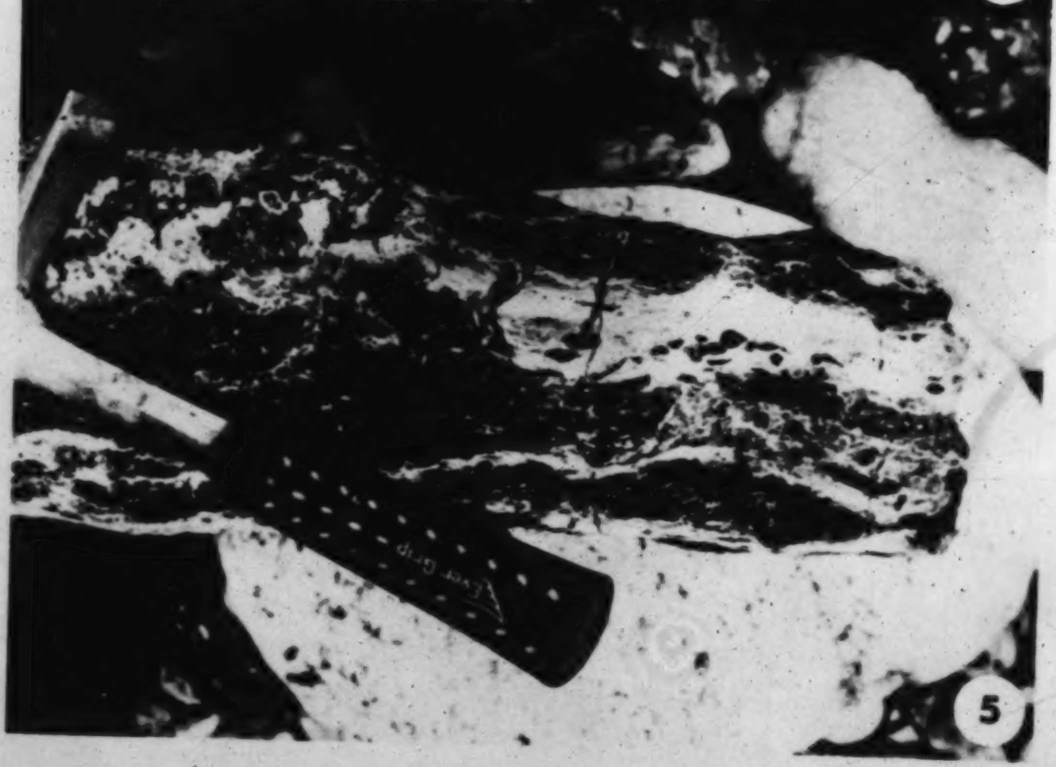

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mainly decomposed, peaty material tended to be blocky and freshly broken surfaces had a black, but dull, appearance, giving the impression of a coarser texture.

It was found that the darkest blocks of chert came from the lower levels of the outcrop, while those of the upper layers were quite pale. Most material, then, was chosen from the lower chert layers. In the event that considerable lateral variation may occur within any one layer, chert blocks were retrieved from the greatest horizontal extent accessable.

All layers of chert have been fractured one or more times since deposition. These cracks now contain blue, white, or red siliceous in-fillings. Frequently this fracturing and subsequent cementing has reduced the chert to breccia that contains so disrupted a fossil assemblage as to be useless.

Fortunately the layers of chert have been broken up by recent weathering and blocks of various sizes are easily obtained. Blocks of chert are quite hard and difficult to break and any attempt to do so causes the chert to shatter and thus reduce its value for study.

Since few of the blocks had been exposed and weathered long enough to reveal the plants contained, a large proportion of the collection was taken with little idea of what was to be found within. The characters described above are by no means rules, for well-preserved and valuable plants can be found in blocks of a wide range of color, shape, size, and texture. When mass collecting, however, it is desirable to obtain large quantities of the most productive material, and by following these guidelines, it is possible to return with a minimum of "waste" rock.

Upon initial observation, the plant fragments appear to be preserved in a matrix of silicified mud. However, upon closer examination, it can be seen that this background material is composed of small fragments of wood, leaves, pollen grains, and other organic debris. There is an apparent lack of inorganic detrital material of any kind. Preserved plant organs probably fell directly into this organic debris shortly before or during silicification. The silicates only penetrated the top several inches of debris on the bottom of the ancient marsh and formed a layer of chert which lay on a thickness of peat that would later be compressed to lignite. There appears to have been little or no compaction of the infiltrated layer, for plant parts show almost no evidence of crushing or distortion, and the particles of the organic matrix are quite loosely arranged. The lack of inorganic material indicates an absence of stream flow into the marsh. Thus, plant organs found in the chert represent parts of a plant community that grew adjacent to the depositional area. Some of the rhizomes and roots possess rootlets that ramify through the matrix and have been preserved *in situ*.

The Clarno chert appears similar to the Ashnola chert in the nature and quality of preservation. As noted previously, the color of the Clarno chert is grey due to the presence of volcanic ash. The cherts of the Deccan Intertrappean series, however, generally compare less favorably with the Ashnola chert. A large number of the localities yield only small quantities of material showing poorly preserved plant parts, although there is an abundance of material found at Rajahmundry, Sausar, and Mohgaon Kalan. At these three localities there is a great diversity of well-preserved plant parts. However, there is usually not an adequate amount of the original organic material remaining in the specimens from even these rich localities to allow the preparation of acceptable cellulose acetate peels. Thin sections must be made in order to study specimens and serial sections are not easily prepared. Serial photographs, using reflected light, and camera lucida drawings of specimens exposed by progressive grinding, techniques practiced frequently (Chitaley, 1955; Prakash, 1956; Verma, 1956; Paradkar, 1973), cannot provide necessary detail nor stand critical examination. In general, the quality and nature of preservation is comparable to that of the "grey chert" of the Ashnola locality.

All specimens figured in the text are deposited in the paleobotanical collection in the Department of Botony, University of Alberta, Edmonton.

Methods

Blocks of chert are first examined for surface evidence of embedded plant material. If plant parts are visible, blocks are cut in order that cross sections of axes will most frequently be obtained. If there are no plant organs to be seen, or if those that are seen give no indication of their orientation, then blocks are cut such that the saw kerf is perpendicular to the bedding plane. Blocks are cut into slabs approximately 2 cm. in thickness.

As noted under "Materials", the Ashnola chert is found in a range of color from grey to black. The variation in color is caused by differences in the amount of the original organic residues remaining in the specimens. As a result of these differences, grey and black samples cannot be treated in the same manner.

Specimens in grey blocks, which lack organic residues, must be thin sectioned for study. Thin slices are cut from slabs with a trim saw, fixed to glass slides with thermal plastic, and hand ground until translucent.

Black blocks, however, retain much of their organic material and lend themselves well to study by a modification of the cellulose acetate peel technique of Joy, Willis, and Lacey (1956). Modifications of this technique include etching specimens in full strength, commercial grade (48%) hydrofluoric acid (HF) for 60 to 120 seconds and then neutralizing in a saturated aqueous solution of sodium bicarbonate ($NaHCO_3$). It was desirable to leave the specimens submersed in $NaHCO_3$ for at least 15 minutes in order that most of the HF be removed prior to handling.

Cellulose acetate film of .003 inches thickness was found most suitable, for it resists tearing more so than thinner film, but is itself thin enough to allow critical microscopic examination under oil. Prior to mounting on microscope slides, peels may be demineralized in full strength HF for one minute, neutralized, rinsed, and dried. Peels can be mounted in Harleco Synthetic Resin (HSR) or Permount, and are comparable in quality to the finest ground thin sections.

Bulk maceration with full strength HF was attempted by Miller (1973) in an effort to retrieve pine needles from the matrix, but was found to be completely unsuccessful. The siliceous matrix is apparently all that holds the organic residues together, and the removal of this matrix results in a total loss of structure. This technique, however, is useful in obtaining palynomorphs (Boneham, 1968).

Any attempts thus far to fracture the blocks along the surfaces of leaves or other organs in hopes of finding planes of least resistance have proven unsuccessful. Blocks fracture along ancient fracture lines that are now in-filled with silicates, or fracture conchoidally, showing no respect for the plant parts contained.

CHAPTER 4

SYSTEMATICS

Class: Filicopsida
Order: Filicales
Family: Polypodiaceae
Sub-family: Dennstaedtioideae

Dennstaedtiopsis aerenchymata Arnold and Daugherty (Figs. 6-18)

DESCRIPTION - Rhizomes and petioles of this polypodiaceous fern are common in the chert, occasionally being the dominant form of vegetation present, but usually found as a minor component in association with other types of plants. Identification was based on comparisons with material described by Arnold and Daugherty (1964), which is the only other report of this species.

The solenostelic rhizomes (Fig. 7) are cylindrical, 5-12 mm in diameter, possess aerenchymatous tissue in both the pith and cortex, and are covered with multicellular hairs (Fig. 8). Petioles (Fig. 9) are naked, possess aerenchyma, and arise singly and at widely spaced intervals. Each petiole has a single trace, which Arnold and Daugherty described as having "... the shape of an inverted bowl with bulbous base and flared rim." Plantlets are often associated with the production of petioles (Figs. 12-17).

Xylem elements are mostly scalariform, but spirally thickened elements were reported in protoxylem cells by Arnold and Daugherty (1964). Xylem maturation is exarch with several clusters of protoxylem cells found around the metaxylem. From these protoxylem points arise the root traces (Fig. 7). To both the interior and exterior of the xylem are identical series of tissue zones (Fig. 18). Immediately adjacent to the xylem is a phloem zone. A single layer of cells of the pericycle separates the phloem from the endodermis and is distinguishable from the former by the darker contents of the cells and from the latter by the vast difference in size. The cells of the endodermis are minute and often not recognizable. A layer of weakly developed sclerenchyma just a few cells thick separates the endodermis from the aerenchyma. The aerenchyma is composed of radially elongate air spaces separated by uniseriate partitions. Interior to the inner aerenchyma is a solid pith of vertically elongate cells. Next to the outer aerenchyma is a thin band of solid, parenchymatous cortex followed by a very weakly developed outer layer of sclerenchyma. A soft, outer cortex only a few cells thick lies exterior to this and is covered by an epidermis bearing simple, multicellular hairs of a variable density.

DISCUSSION - The identification of Dennstaedtiopsis aerenchymata by Arnold and Daugherty (1964) was based solely on vegetative features, so a definite affinity with the extant genus Dennstaedtia could not be determined. As in the Clarno material, no sporangia or well-preserved laminae were found, although laminae without recognizable structure are occasionally found attached to midribs (Fig. 11).

Higher portions of the fronds must have undergone decay prior to infiltration. However, Arnold and Daugherty found that marked vegetative similarities exist between the fossil and Dennstaedtia and state (1964, p. 68):

> "The accumulated evidence, incomplete though it is, does seem, however, to point quite convincingly to a place in the subfamily Dennstaedtioideae of the Polypodiaceae. Relationship with any particular genus is less certain, though there are unmistakable resemblances with certain species of Dennstaedtia."

The most apparent difference between the fossil and Dennstaedtia is an adaptation to an aquatic habitat (aerenchyma) exhibited by the former that is unknown in living Dennstaedtia. However, Kaplan (1970) has found that leaf anatomy may vary greatly even among populations of a single species. This difference, then, may be of minor significance.

Order: Filicales

Incertae sedis

Fern A (Figs. 22-25)

DESCRIPTION - Petioles of this fern are ovoid, with an adaxial groove. A sclerenchymatous hypodermis surrounds a solid cortex. The stele is comprised of two hippocampus-shaped traces and is referred to as the *Onoclea*-type of stelar configuration by Ogura (1972) (Figs. 20-25). The traces fuse at more distal levels (Fig. 25). No rhizomes or laminate pinnules have been found.

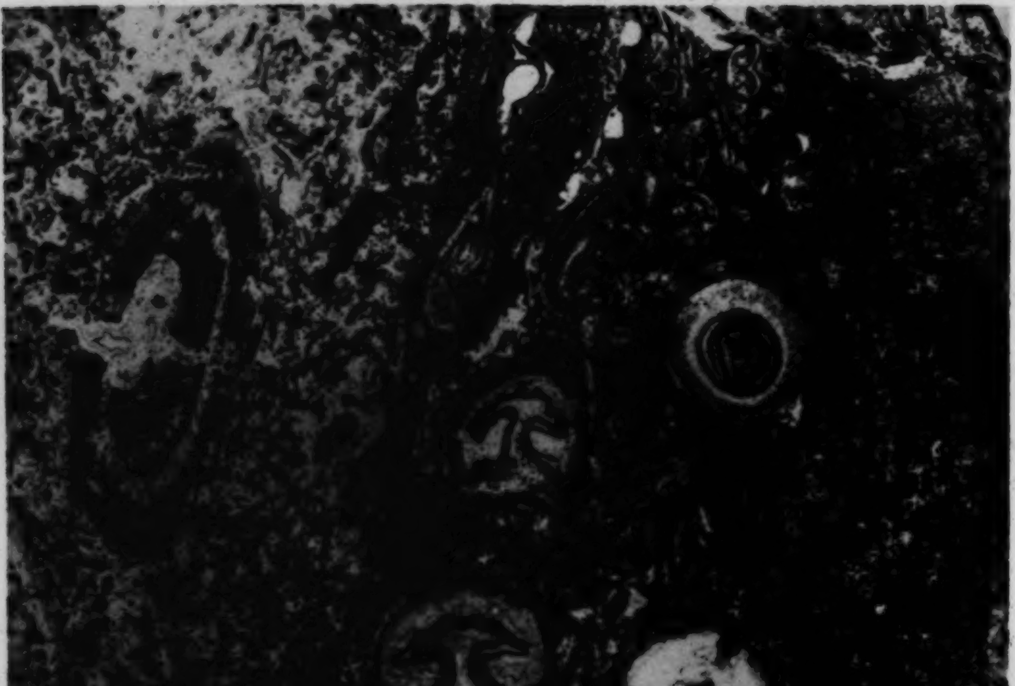
DISCUSSION - Ogura (1972) has found that the *Onoclea*-type of stelar configuration occurs in the Aspidiaceae (*Matteuccia*, *Athyrium*, *Diplazium*, *Onoclea*, *Woodsia*, *Peranema*, *Hypodematium*, *Cystopteris*, etc.) and in a few species of the Pteridaceae (*Onychium*, *Pteris*, *Adiantum*).

The most distal portions of these petioles, where the traces have fused, appear very similar to the smallest petioles of *Dennstaedtiopsis aerenchymata*. This is especially true where the preservation is poor, but under conditions of good preservation they are distinguishable by such characters as the greater degree of endodermal wall thickening in the unidentified fern. This fern is not common in the chert and does not appear to be associated with *Dennstaedtiopsis*.

Fern B (Figs. 19-21)

DESCRIPTION - Both large petioles and rhizomes of this fern are represented, but none of the more distal portions of the fronds have been found. Preservation of the rhizome is poor and has not permitted an accurate description beyond identifying it as a dictyostele (Fig. 19). Petioles, on the other hand, are well-preserved and clearly show an outer, sclerenchymatous layer surrounding a primarily aerenchymatous cortex (Figs. 20 and 21). The stele is composed of several bundles, each surrounded by its own endodermis. These bundles are assembled in a bowl-shaped

Fig. 6. Dennstaedtiopsis aerenchymata. Cross sections of several rhizomes and petioles showing variability in the size of rhizomes and the difference in size between proximal and distal portions of the petioles. P1094 B bot X 4.3.



Figs. 7 - 11. Dennstaedtiopsis aerenchymata. (h = hairs; l = lamina; m = midrib; r = root; rt = root trace.)

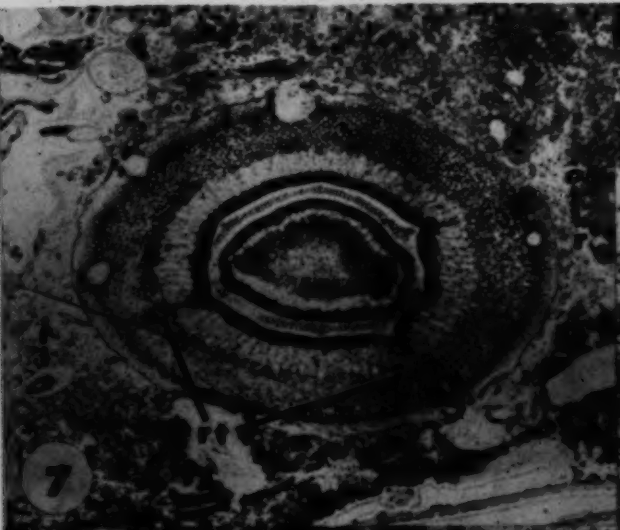
Fig. 7. Cross section of a rhizome showing general features. Note root traces and departing roots. P1194 F bot X 8.

Fig. 8. Cross section of rhizome showing cortex and epidermis. Note multicellular epidermal hairs. P1194 C top X 22.

Fig. 9. Cross section of large petiole showing general features. Note the recurved, adaxial arms of the vascular strand. P1194 C top X 13.

Fig. 10. Midrib attached to the distal portion of a petiole. P1233 C bot X 34.

Fig. 11. Midrib with attached lamina. This illustrates the poor quality of preservation in this portion of the frond. P1247 E bot X 34.



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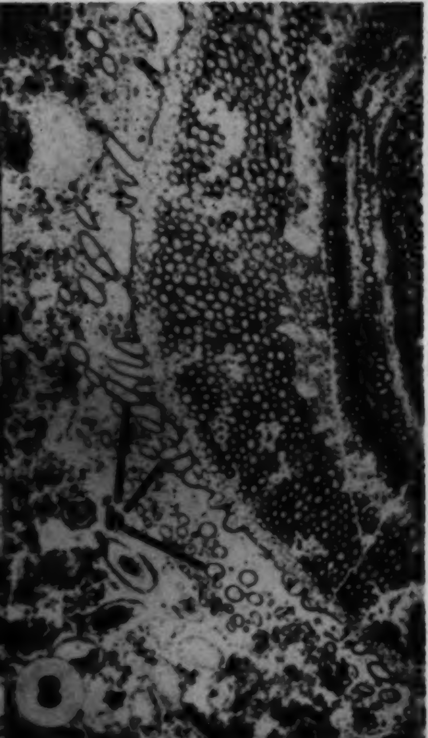

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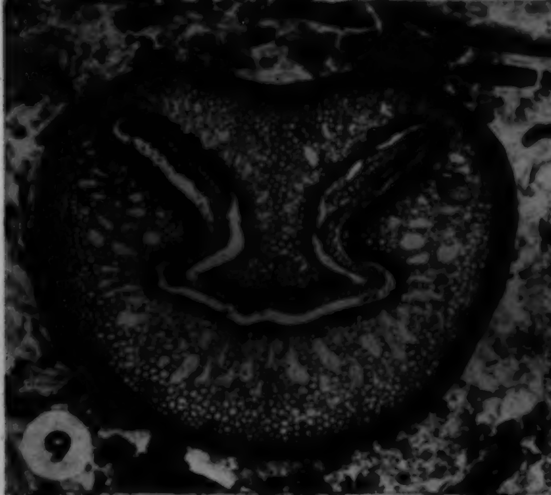

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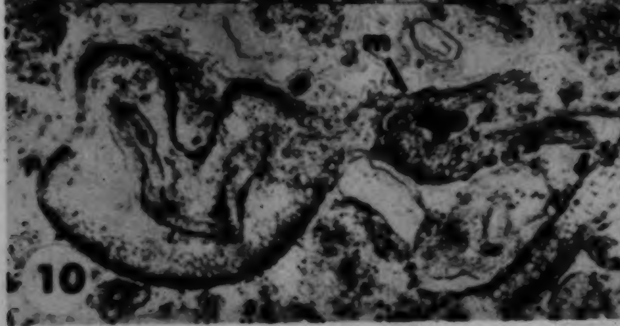

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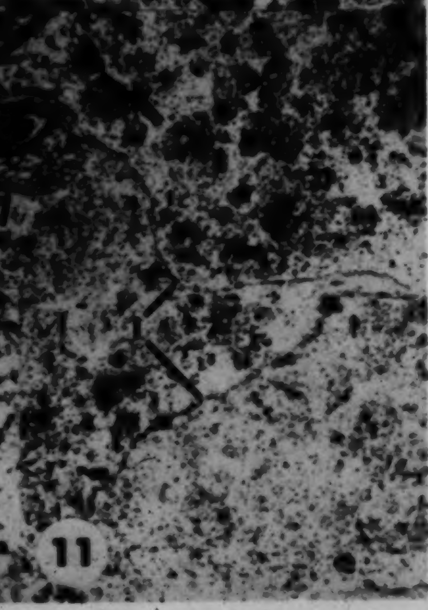

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Figs. 12 - 17. *Dennstaedtiopsis aerenchymata*. Serial sections of a rhizome showing the production of a leaf and a plantlet. Fig. 17 has been taken from a second specimen due to decreasing quality of preservation in a similar portion of the rhizome used for Figs. 12 - 16.

Fig. 12. Cross section of the rhizome showing the still intact vascular cylinder. Note the expansion of vascular tissue on the upper side of the stele. P1233 A21 X 6.

Fig. 13. The vascular cylinder has opened in the region where the enlargement occurred. The trace is departing to the left. P1223 A6 X 6.

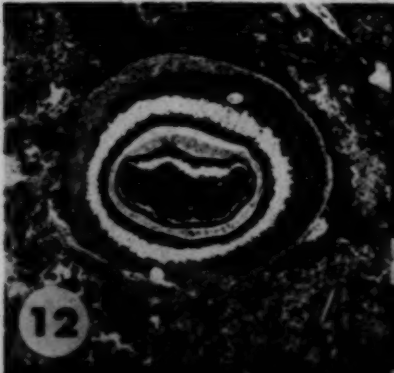
Fig. 14. As the gap in the vascular cylinder widens, a plantlet trace begins to form as a bulge in the developing leaf trace. This and the following two figures were taken from opposite sides of the saw kerf to Figs. 12 and 13. For this reason Figs. 12 and 13 appear as mirror images to Figs. 14 - 16. P1223 B1 X 6.

Fig. 15. The stele of the plantlet is nearly free from the parent rhizome. Note root production by the plantlet. P1223 B7 X 6.

Fig. 16. The plantlet is now departing, but the quality of preservation is deteriorating. Serial sectioning of this specimen was discontinued. P1223 B21 X 6.

Fig. 17. The series is continued by a second specimen showing leaf trace departure. The vascular cylinder of the rhizome is now closed. P1194 G top X 6.

Fig. 18. *Dennstaedtiopsis aerenchymata*. Cross section of the vascular cylinder of a rhizome. (a = aerenchyma, e = endodermis, pc = pericycle, ph = phloem, scl = sclerenchyma, x = xylem). P1204 K bot X 58.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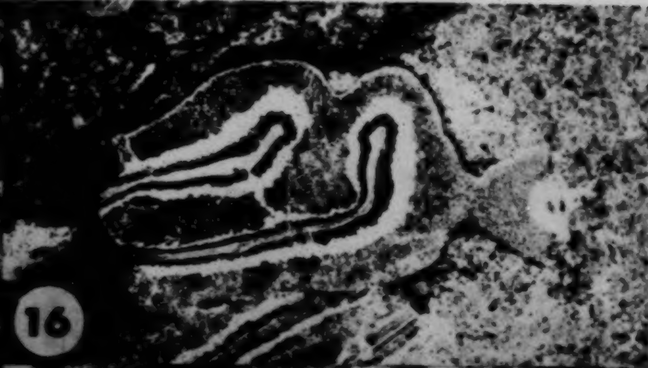
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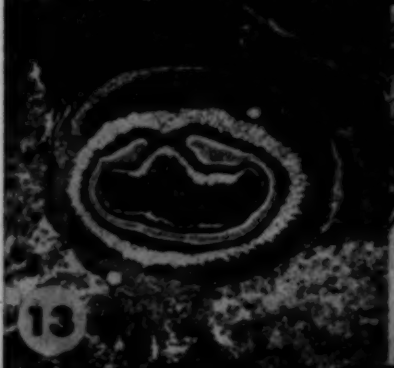
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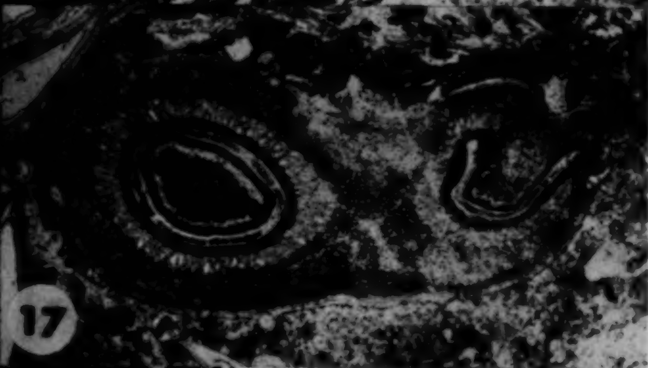
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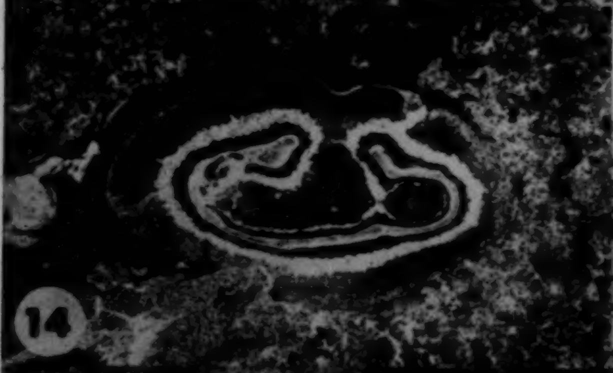
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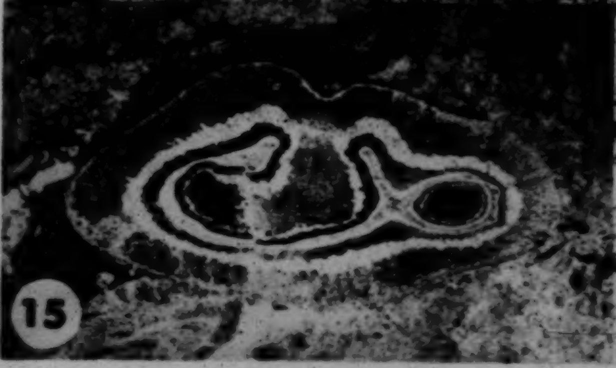
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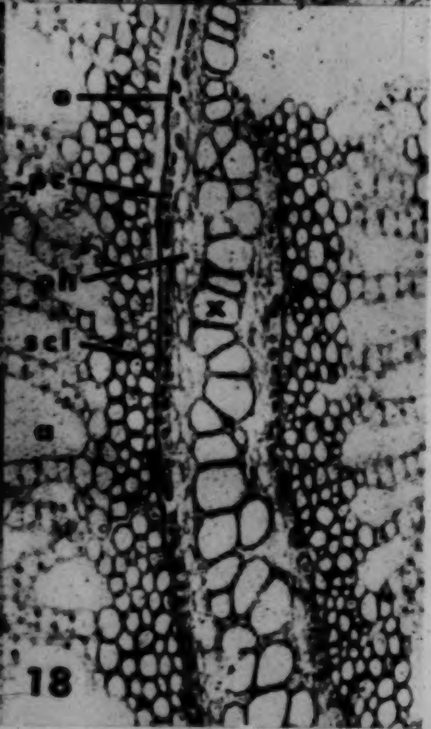
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configuration. The two bundles forming the mouth of the bowl (adaxial traces) are considerably larger than the others and possess a recurved, adaxial arm. Other traces are bar- or C-shaped. This type of stelar configuration is known as the Aspidium-type (Ogura, 1972).

DISCUSSION - The Aspidium-type of stelar configuration is found in the Aspidiaceae (Dryopteris, Polystichum, Aspidium, Acrophorus, Elaphoglossum, Bolbitis, Egenolfia, etc.) and the Blechnaceae (Blechnum, Doodia, Brainea, Woodwardia, etc.) (Ogura, 1972). Rhizomes with dictyosteles of various types are common in both families.

Ogura (1972) has proposed that the Onoclea-type of stele gave rise to the Aspidium-type by a proliferation of traces. In fact, the most distal portions of the latter type, where the smaller, medial traces have fused to the larger, adaxial ones, actually appear to have the Onoclea-type of configuration. It is possible, then, that Fern A, which is only represented by small petioles, may be the distal portions of petioles of Fern B. As yet, there is little evidence to support or negate this primarily due to the infrequency with which these forms are found. They have not yet been found associated with one another, and aerenchyma has not been seen in Fern A, so they are here treated as separate entities.

Class: Coniferopsida
Order: Coniferales
Family: Pinaceae

Pinus (Figs. 26-53)

Remains of Pinus can be found in nearly every chert layer and have been the subject of a detailed study by Miller (1973). Miller proposed the names Pinus arnoldii and P. similkameenensis for reproductive and vegetative remains respectively. Although there is only one type of each organ present, Miller found that vegetative and reproductive organs appeared to represent different subgenera of the genus Pinus and was reluctant to place them in the same species.

Pinus arnoldii

DESCRIPTION - This species is based on seed cones that measure 5 - 6 cm in length and 2 - 2.5 cm in diameter. The wood of the vascular cylinder has an abundance of resin canals and an indistinct growth ring. The cortex is comprised of three layers: an inner, parenchymatous layer of small cells; a middle cortex of large parenchyma cells and resin canals; and an outer layer of sclerotic cells (Fig. 27).

Bract and scale traces arise as a complex which divides into the respective traces in the outer cortex

Figs. 19 - 21. Order Filicales, Incertae sedis (Fern B).

Fig. 19. Cross section of a rhizome producing leaves. Two petiolar steles are seen in the right and left regions of the rhizome while a petiole has recently departed above. Note that aerenchyma is not apparent in the most proximal portions of the petiole, but well developed aerenchyma is found in more distal regions. P1247 C top X 5.

Fig. 20. Cross section of a petiole showing well developed aerenchyma and a dissected stele. Note the recurved arms of the two adaxial bundles. P1247 B bot X 15.

Fig. 21. Cross section of a petiole showing fusion of a small, median vascular bundle to an adaxial bundle. P1247 D top X 15.

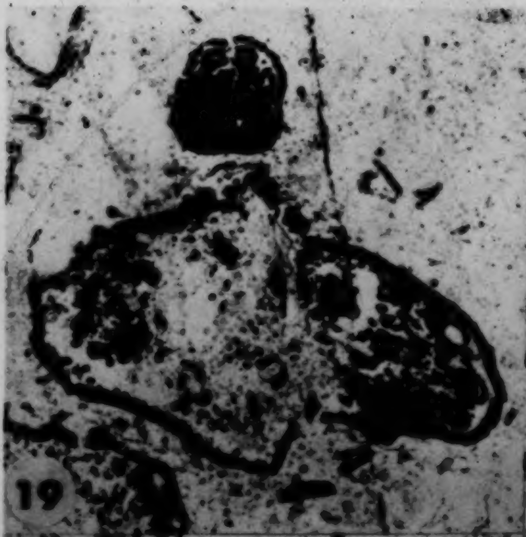
Figs. 22 - 25. Order Filicales, Incertae sedis (Fern A).

Fig. 22. Cross section of a petiole showing general features. Note the two hippocampus - shaped traces and the absence of aerenchyma. P1179 D top X 28.

Fig. 23. Cross section of a small petiole. P 1182 I bot X 39.

Fig. 24. Cross section of a very small petiole which is still supplied by two vascular traces. P1182 I bot X 63.

Fig. 25. Cross section of a very small petiole showing fusion of the abaxial margins of the traces. P1182 J top X 70.



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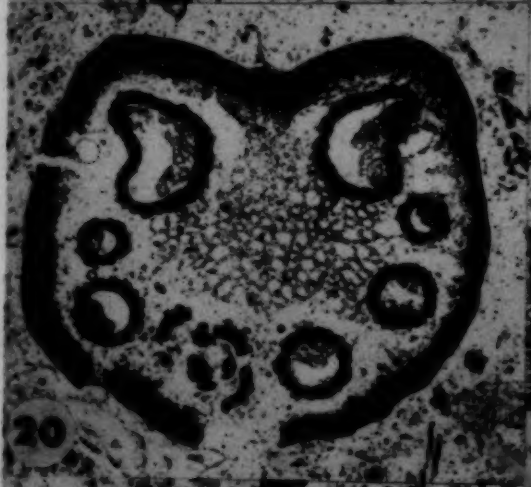

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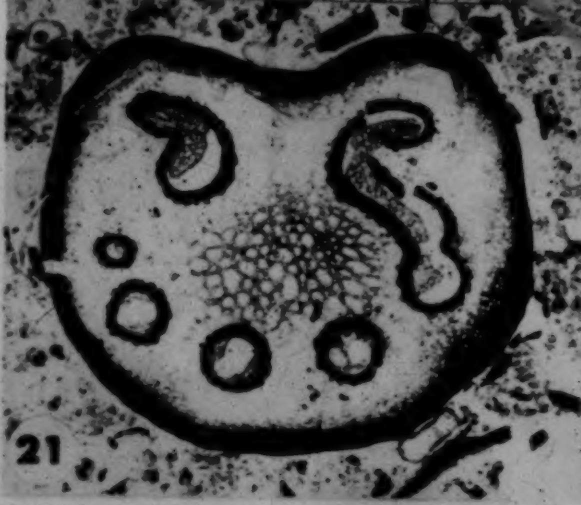

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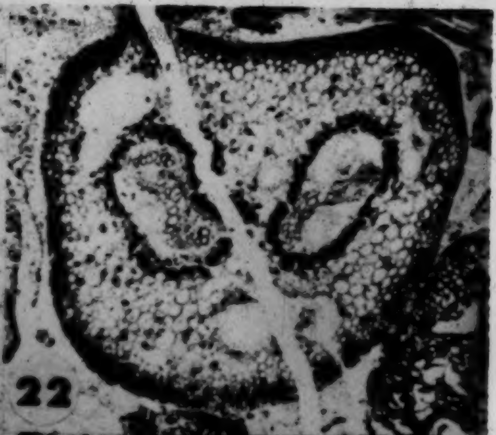

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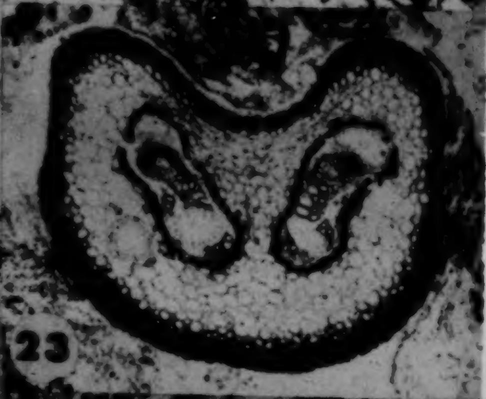

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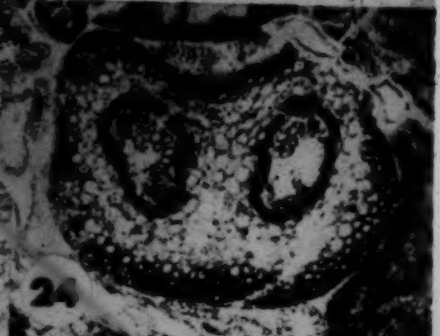

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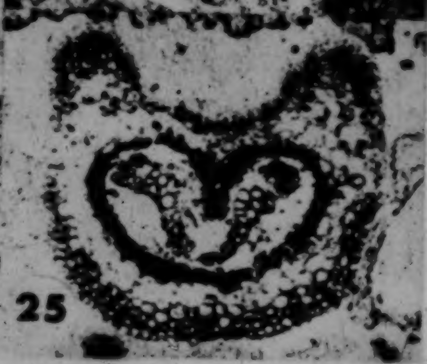

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of the cone axis. The bract trace retains its terete shape as it diverges from the compound trace and passes into the trace. The scale trace, however, loses its circular outline and becomes flattened upon entering the scale and eventually divides into 10 to 15 traces.

The bracts are 4 - 5 mm long and are free of the scale for its entire length (Fig. 28). The ovuliferous scales are 16 - 20 mm long and 4.5 - 6.0 mm wide and have 2 adaxial seed cavities near the base and an inflated apex with an apophysis and an umbo (Fig. 28).

Seeds have been discovered both in cones (Fig. 30,32), and in a dispersed state (Fig. 31). A wing (Fig. 32) is present before dispersal, but has not been found on isolated seeds.

DISCUSSION - That the cones are attributable to the genus Pinus was determined by Miller (1973) on the basis of the presence of an inflated apex and umbo and the restriction of resin canals of the scale base to the abaxial side of the vascular tissue.

Miller had more difficulty in relating Pinus arnoldii with an extant subgenus or section. The inflated scale apex and dorsal umbo are suggestive of the subgenus Pinus, although a few species of the section Parrya, subgenus Strobus, have similar features. Internal structure including the nature of the outer cortex is similar to the subsections Contortae, Oocarpae, and Sylvestres of the section Pinus, subgenus Pinus. However, most species of the Contortae and *Oocarpae* produce serotinous, asymmetrical cones and *P. arnoldii* appears to have had neither feature. Miller chose species of the subsection *Sylvestres* as those to which *P. arnoldii* showed most similarity.

Miller notes, however, that *P. arnoldii* does show external similarity to certain species of the section *Parrya* of the subgenus *Strobus*. In both cases cones are long and cylindrical and scales have an inflated apex and dorsal umbo. Miller doubts a close relationship between *P. arnoldii* and species of the section *Parrya* since *P. arnoldii* has small seeds, large pith cells, a small gap left by the departure of the bract-scale trace complex, and the branching of this complex in the outer cortex rather than the inner cortex as in the extant species.

Miller, then assigned *P. arnoldii* to the subsection *Sylvestres*, section *Pinus*, subgenus *Pinus*, but acknowledged the possibility of other affinities.

Pinus similkameenensis

DESCRIPTION - Small and large stems, short shoots and needles, and roots assignable to this species are abundant in the chert and are invariably present when cones of *P. arnoldii* are found.

Needles and Short Shoots - Needles are approximately 0.5 mm wide, have a single vascular trace, and are borne in fascicles of five (Figs. 46, 48). Miller determined their length to be at least 2.3 cm, but could find no intact leaves, so their actual length was probably much greater (possibly several times that length).

The vascular bundle is surrounded by transfusion tissue. External to this is a prominant endodermis. Mesophyll is composed of very irregularly shaped cells with dentate walls. Beneath the epidermis is a 1 - 2 cell thick layer of hypodermal fibers. Two resin canals are found on the dorsal side of the leaf and are usually external. Stomata are absent from the dorsal surface, but are present in rows on both ventral surfaces (Miller, 1973).

Dwarf shoots are 1.0 - 1.5 mm in diameter and about 2.0 mm long. Miller could find no needle clusters with intact fascicle sheaths and presumed that they were deciduous as they are in modern species of the subgenus Strobus. Some fascicles retaining their sheaths have been found in the present study (Figs. 45, 46). The immaturity of the needles attached to these fascicles lends support to Miller's premise that the sheaths were deciduous.

Wood - Both vertical and horizontal resin canals are present and both are surrounded by thin-walled epithelial cells (Figs. 35, 37). Rays are uniseriate and 1 - 8 cells tall or, where a resin canal is involved, biseriate and 10 - 16 cells tall (Fig. 38). Tracheids have uni- or biseriate circular bordered pits on the radial walls (Fig. 39) and smaller, scattered circular bordered pits on the radial walls (Fig. 39) and smaller, scattered circular bordered pits on the tangential walls (Fig. 38). In the cross-field, ray parenchyma cells were found by Miller to possess 1 - 4 circular, simple pits (Fig. 40). In the present study I have also found fenestriform pitting in the cross-field (Fig. 41). Ray tracheids (Fig. 42) are present but not common. They have smooth walls and small circular bordered pits.

The cortex has been preserved in a number of the smaller stems and it is possible to recognize phloem and cork zones. Miller has followed dwarf shoot traces through the cortex to the bases of dwarf shoots. Although there have been no dwarf shoots found attached to the twigs, evidence presented by Miller is strongly suggestive of their former connection.

Roots - Pinaceous roots are often found in association with remains of _P. arnoldii_ and _P. similkameenensis_ (Figs. 43, 44). These roots are di-, tri-, and tetrarch and range in size from 3 mm to 3 cm in diameter. Wood and cortex is frequently very well preserved. Resin canals (Fig. 44) are abundant and are lined with thin-walled epithelial cells. Many roots possess lateral roots still in attachment (Fig. 43) and have been preserved _in situ_.

The presence of resin canals with thin-walled epithelial cells allows these roots to be referred to the genus _Pinus_. On the basis of association with remains of _P. similkameenensis_ and of there being no other types of pinaceous remains present, these roots are assigned to *P. similkameenensis* (since the position of *P. arnoldii* is presently in question and all other pinaceous vegetative remains have been referred to *P. similkameenensis*, it is best to assign the roots to *P. similkameenensis*).

DISCUSSION - It appears that all vegetative organs belong to a single species. Some of the wood that I have examined appears to differ from that which Miller examined in that cross-field pitting is fenestriform rather than being composed of smaller, circular pits. However, there is as yet no other evidence for there being two types of wood present and I suspect that this difference reflects natural variability in the wood of *P. similkameenensis*. The discovery of fenestriform pits does alter the interpretation of the wood proposed by Miller (1973).

Both needles and wood were identified as belonging to the subgenus *Strobus*. Miller found the needles to be anatomically inseparable from those of certain living species of the section *Strobus* (*Pinus monticola*, *P. parviflora*, *P. puece*, *P. strobiformis*, and *P. strobus*). Harlow (1931) described the needles of these species as having a generalized structure from which other quinate needle types have evolved. The presence of such a needle type in *P. similkameenensis* of Eocene age lends support to Harlow's (1931) theory.

The fossil wood was referred to the subgenus *Strobus*

(Miller, 1973) on the basis of smooth-walled ray tracheids and of pitting on the tangential walls of the tracheids. The only point of dissimilarity is the much greater number of ray tracheids found in the modern species. Within the subgenus *Strobus*, Miller identified the wood as belonging to the section *Parrya*. He found the major difference between members of the section *Strobus* and the fossil to be the lack of fenestriform pits in the cross-field of the latter.

These findings led Miller to describe the vegetative remains of *P. similkameenensis* as having a combination of features of both sections *Strobus* and *Parrya* of the subgenus *Strobus*. With the discovery of fenestriform pits in *P. similkameenensis*, a much closer relationship to the section *Strobus* is established. Variability in the cross-field pitting in *P. similkameenensis* may prove to be normal in modern species upon further investigation of extant pine, or it may indicate that, vegetatively, *P. similkameenensis* and perhaps the section *Strobus* were less well defined in the Eocene.

Relationships between *Pinus arnoldii* and *P. similkameenensis* - Since Miller (1973) could find only one type of each organ present in his samples, he believed that they may all belong to a single species. Miller states that (1973, p. 117):

> "Such a species would thus have features that are generally regarded as distinctive of the two main subdivisions of the genus, and this mixing of characters would further imply that the subgenera *Pinus* and *Strobus* may not have existed as separate lines of specialization in the Eocene."

However, Miller could not place the organs into one species because an organic connection is lacking and he was not able to make an extensive survey of the Ashnola locality to determine if other types of organs were to be found elsewhere in the outcrop. If two species of Pinus were in the vicinity, two types of at least one organ would be expected to occur in the chert. As yet I have found no organic connection, but there is still only one type of each organ known. This is strong evidence for combining P. arnoldii and P. similkameenensis into a single species. Furtheremore, Miller did notice a resemblance between P. arnoldii and certain species of the subgenus Strobus. Although evidence for a single species is gaining, I believe it is not possible yet to unite P. arnoldii and P. similkameenensis. Further speculation about the relationships between the subgenera Pinus and Strobus should await proof that P. arnoldii and P. similkameenensis are the same species.

Pinus sp.

DESCRIPTION - Pinaceous pollen cones occasionally occur in association with remains of Pinus arnoldii and P. similkameenensis. The cones are ovoid and about 5 mm in length and 3 mm in diameter (Figs. 49, 50). Each microsporophyll bears two abaxial pollen sacs that are usually empty, but some still contain pollen (Fig. 51). Pollen grains are bisaccate and of the *Pinus*-type (Figs. 52, 53). Preservation does not appear to be good enough to allow an anatomical study of the cone axis and microsporophylls.

DISCUSSION - That these cones belong to the genus *Pinus* is indicated by the type of pollen grains present. However, identification within the genus must await detailed study.

Attachment of these cones to associated twigs of *P. similkameenensis* has not yet been found but the close association of these remains and the absence of other types of pinaceous remains in the chert strongly suggests the possibility. If they are found to belong to *P. similkameenensis*, these pollen cones may provide an insight into the relationships between *P. arnoldii* and *P. similkameenensis*. The possibility that all these organs may represent one species is important, for it would represent one of the most completely known species of fossil conifers.

Family: Taxodiaceae

Metasequoia sp. (Figs. 54-73)

Taxodiaceous remains are frequent in the chert and occur as wood fragments, twigs, leaves, and pollen cones. While only one type of each organ is present, the different organs show a combination of features found in two modern genera. Both pollen cones and wood show affinities to extant *Metasequoia*, but the leaves are anatomically most similar to Taxodium.

Pollen Cones

DESCRIPTION - Taxodiaceous male cones are numerous and have been studied in some detail by Rothwell (1975) , and much of the following description has been adopted from his work. The cones are 3.1 - 5.0 mm in length and 1.8 - 3.0 mm in diameter and bear numerous, spirally arranged sporophylls subtended by imbricate, scale-like leaves. Subsequent to the publication of the above-mentioned abstract, Rothwell (personal communication) found that the subtending leaves were decussately arranged and that this pattern did not persist in the sporophylls. Each microsporophyll bears three sporangia filled with spheroid, papillate pollen (Fig. 57). Pollen grains are from 23 to 28 um in diameter. Although microsporophylls are generally not well preserved and cellular detail has not been available, a single, large mucilage duct is clearly evident in each (Fig. 55).

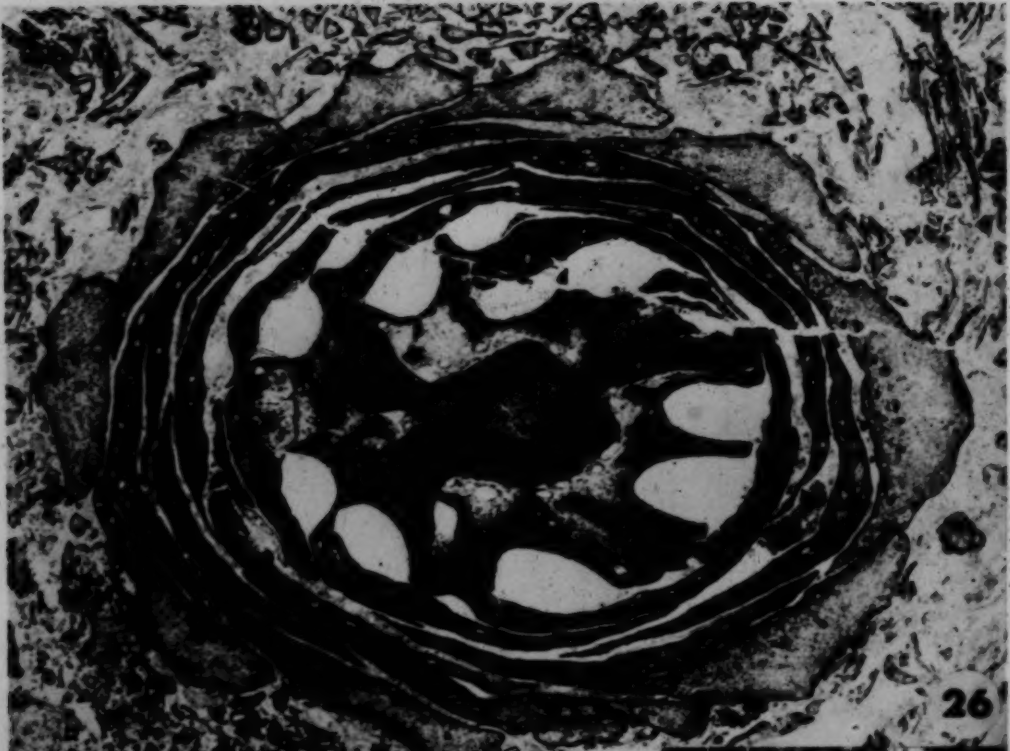
DISCUSSION - Initially Rothwell (1975) believed that the fossil cones were comparable to Metasequoia, Sequoia, and Sequoiadendron. He has since determined that features of scale-leaf arrangement, nature of microsporophylls, and the number of microsporangia per microsporophyll make the fossil cones almost identical to cones of Metasequoia glyptostroboides.

Figs. 26 - 28. *Pinus arnoldii*. (b = bract, rc = resin canal, sa = scale apex, sb = spine base, sc = seed cavity, tc = scale trace complex).

Fig. 26. Cross section at approximately the middle of the cone showing general features. P1040 C top X 4.5.

Fig. 27. Closeup of the cone axis of the specimen illustrated in Fig. 26. Note the departure of two scale trace complexes to the left. P1040 C top X 10.

Fig. 28. Longitudinal section through bracts and scales of f cone showing the inflated scale apex and dorsal umbo. Note the former point of attachment of a spine. The object projecting from this point into the matrix may be the spine, but attachment has not been demonstrated. P1143 A X 9.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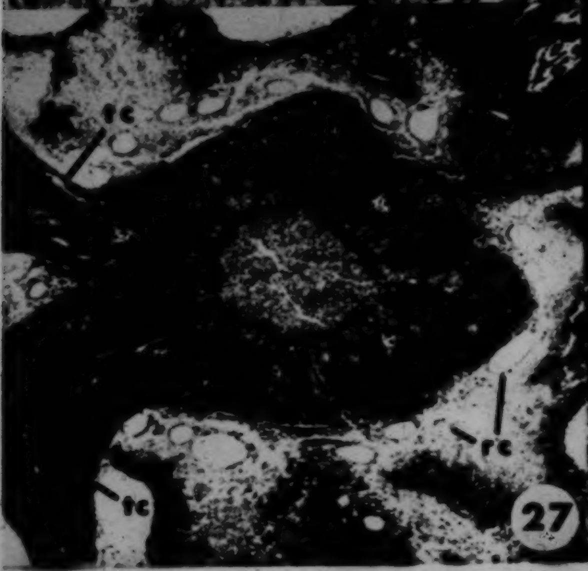
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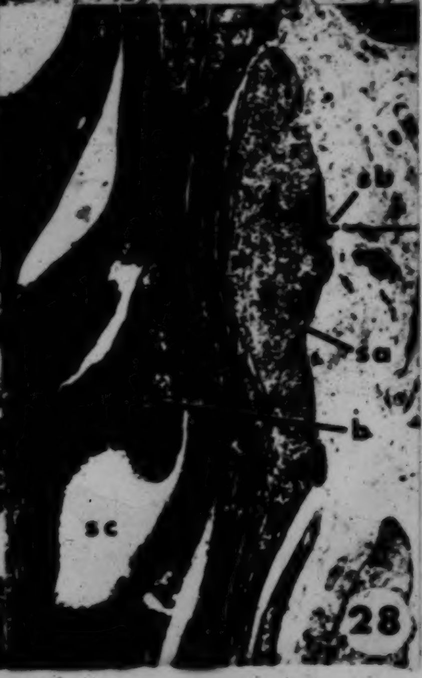
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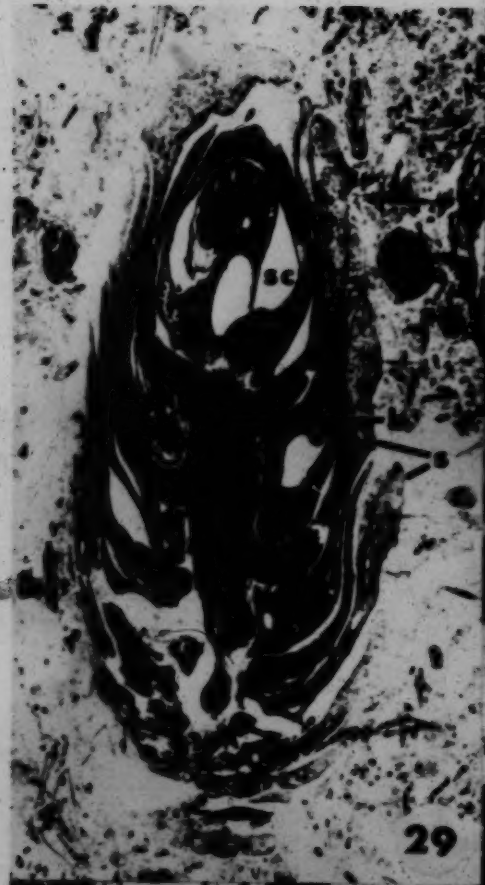
Figs. 29 - 32. *Pinus arnoldii*. (b = bract, s = scale, sc = seed cavity, w = wing.)

Fig. 29. Oblique longitudinal section of a cone showing general features. P1143 A X 3.

Fig. 30. Cross section of a cone with a seed. P1210 I Bot X 3.6.

Fig. 31. Seed in a dispersed state. No wing was found attached to this seed. P1143 E bot X 26.

Fig. 32. Closeup of the seed shown in Fig. 30. Note the attached wing. P1210 I bot X 15.



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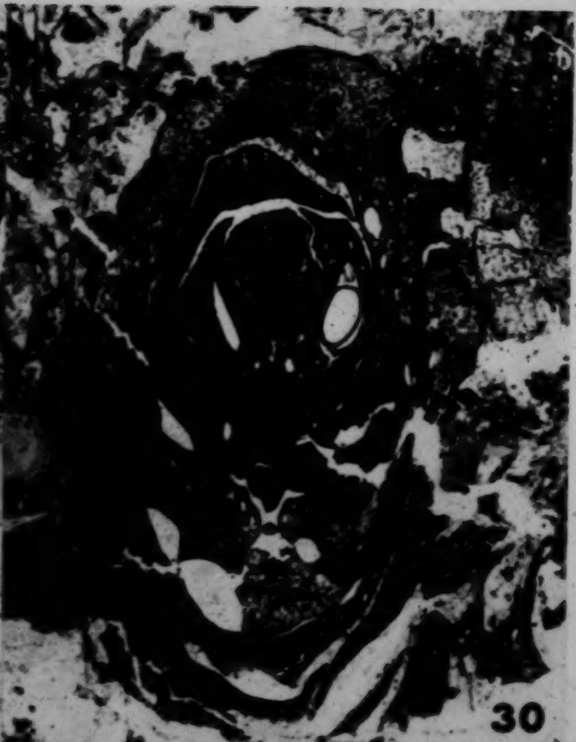

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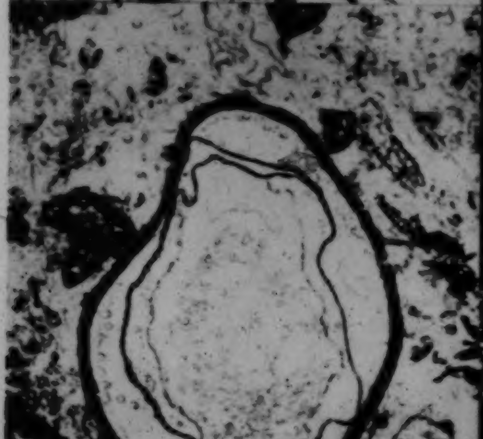

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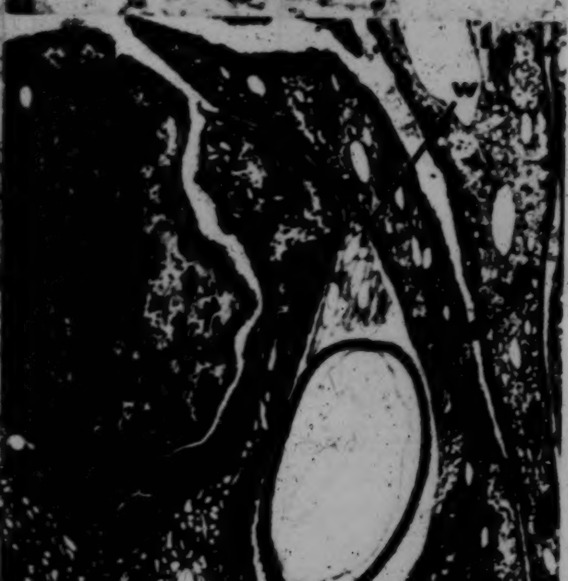

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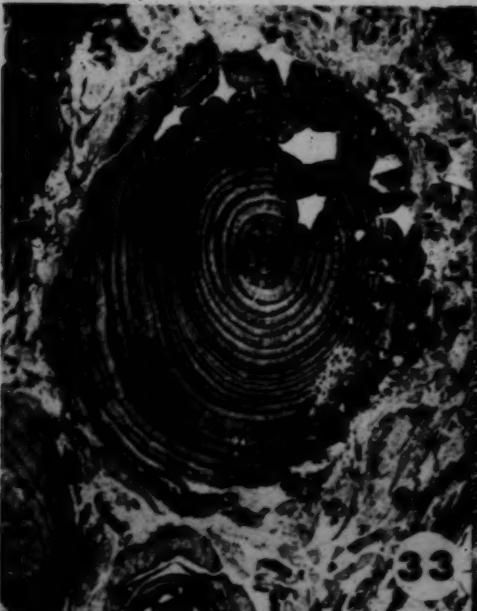
Figs. 33 - 36. Pinus similkameenensis. (sss = short shoot scar, sst = short shoot trace.)

Fig. 33. Cross section of a large, decorticated axis. P1193 A X 2.4.

Fig. 34. Pith region of the stem shown in Fig. 33. P1193 A X 42.

Fig. 35. Portion of secondary wood showing the distribution of resin canals. Note the thin-walled epithelial cells lining the resin canals. P1193 A X 23.

Fig. 36. Cross section of a twig. Note the departure of a short shoot trace on the lower right and the scar left by the abscission of a short shoot on the left. P1210 G bot X 15.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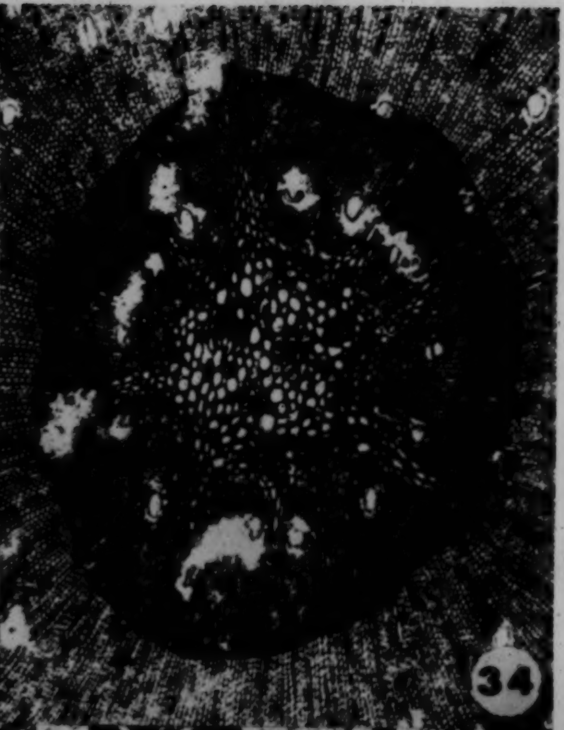
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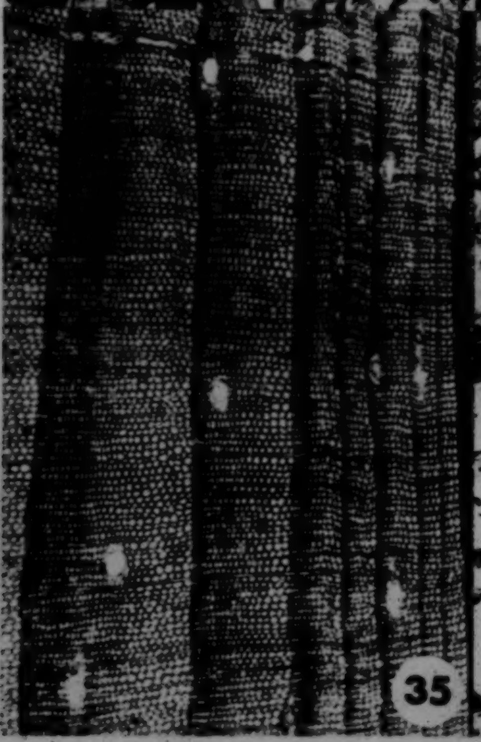
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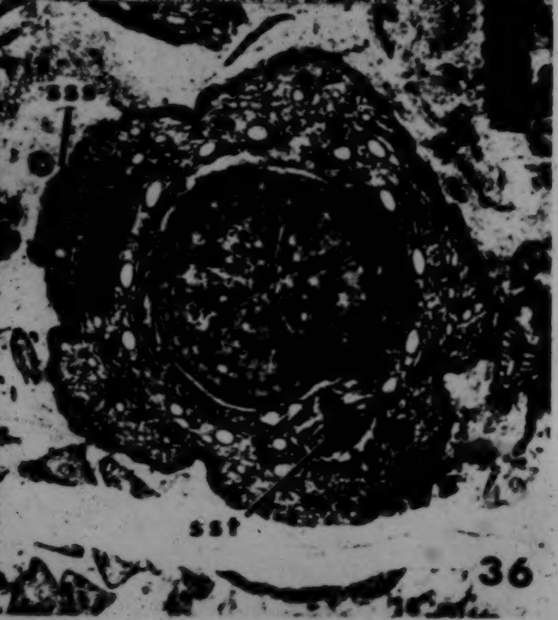
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Figs. 37 - 42. Pinus similkameenensis. Tangential and radial sections of wood. (hrc = horizontal resin canal, tp = tangential pit, vrc = vertical resin canal).

Fig. 37. Tangential section showing heterogeneous ray structure. P1101 I X 38.

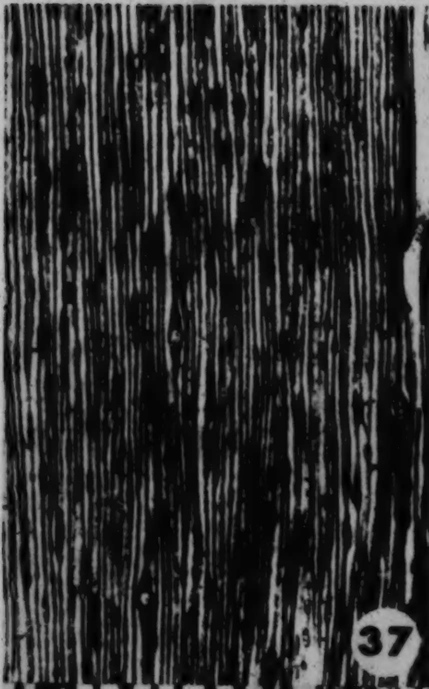
Fig. 38. Enlarged portion (tangential) of Fig. 37. Note the thin-walled epithelial cells lining the horizontal resin canals. Note also the pitting on the tangential walls of the tracheids. P1101 I X 138.

Fig. 39. Radial section showing general features. P1101 I X 38.

Fig. 40. Radial section showing cross-field pitting. The small, circular pits of this specimen closely resemble the pits figured by Miller (1973). P1143 E top22 X 235.

Fig. 41. Radial section showing cross-field pitting. Note the large, fenestriform pits exhibited by this specimen. P1101 I X 340.

Fig. 42. Radial section showing ray tracheids on the margins of a ray. P1101 I X 320.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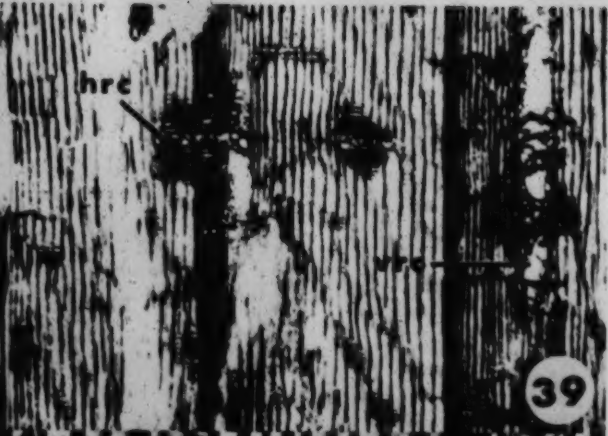

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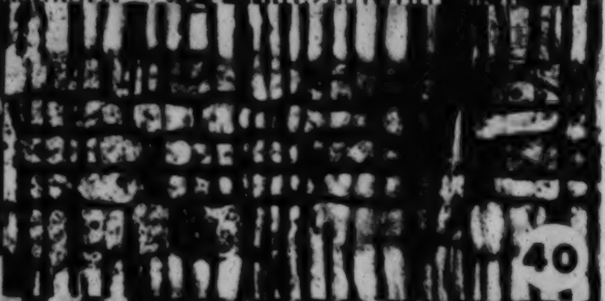
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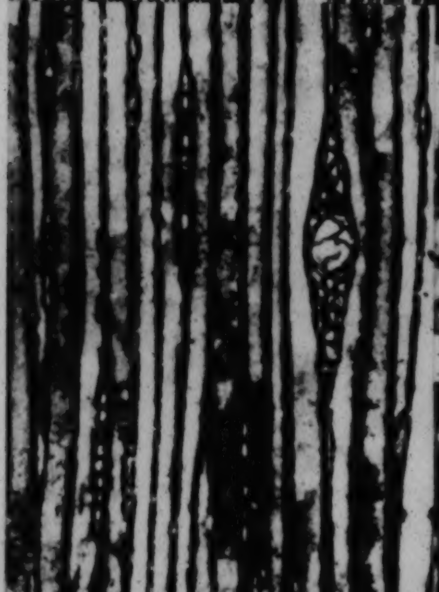
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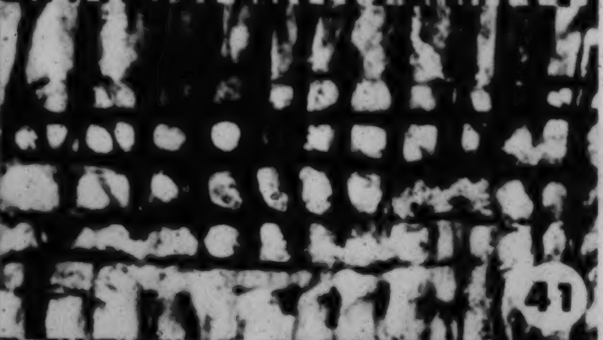
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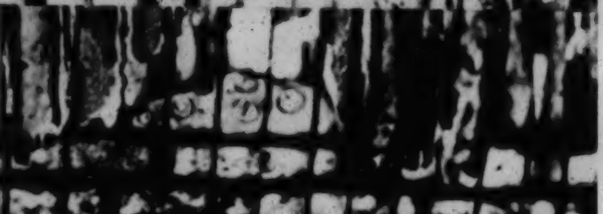
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Fig. 43 - 48. Pinus similkameenensis. (fs = fascicle sheath).

Fig. 43. Cross section of a large root. The attachment of lateral roots suggests that roots of this kind were preserved in situ. P1143 A X 3.5.

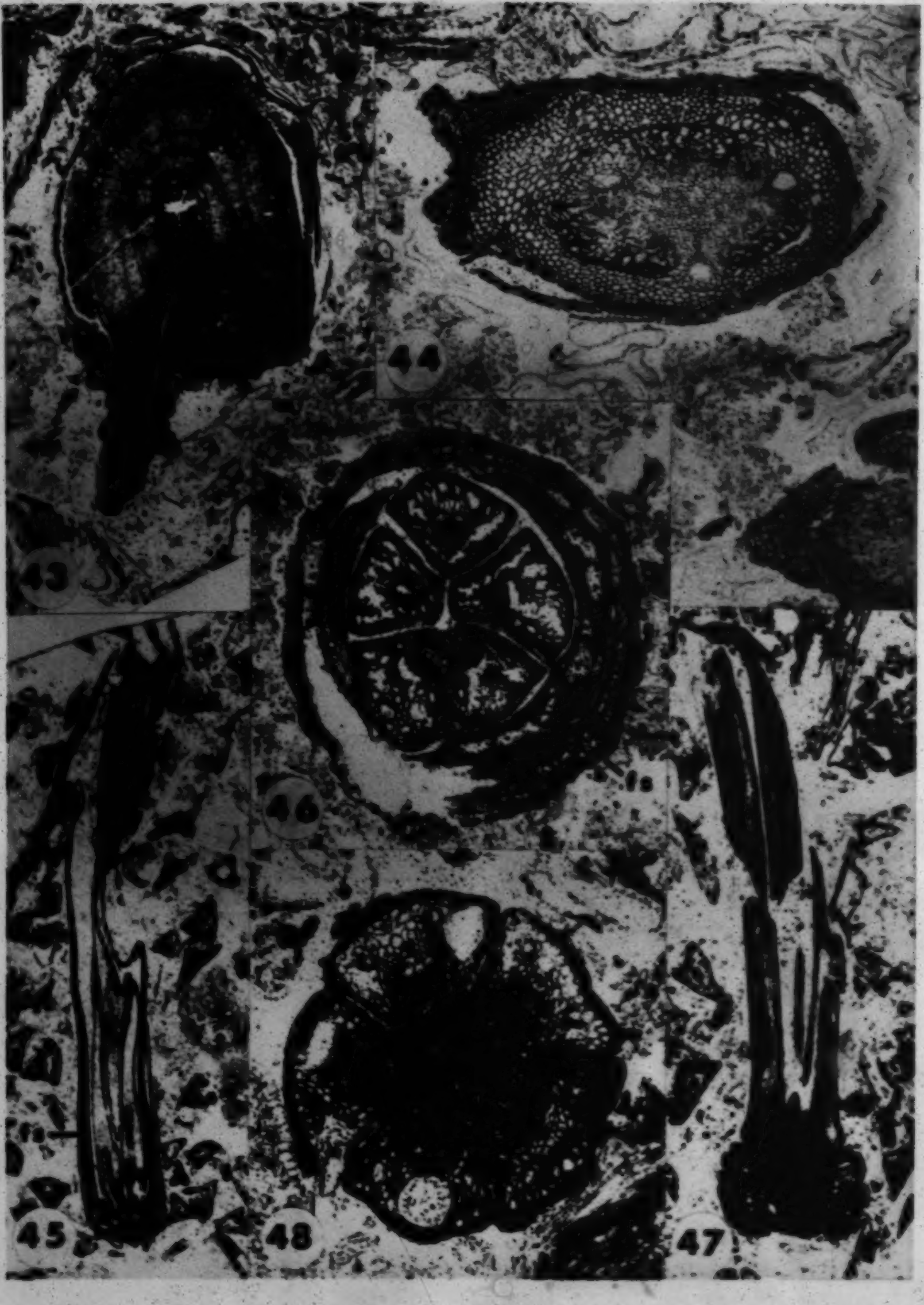
Fig. 44. Triarch rootlet with a small amount of secondary development. Note the resin canals at the tips of each primary xylem arm. P1257 I1 bot X 24.

Fig. 45. Longitudinal section of a young fascicle of pine needles showing the attached fascicle sheath. P1143 F X 10.

Fig. 46. Cross section of a young fascicle of pine needles showing the quinate arrangement and the surrounding fascicle sheath. P1070 C top X 32.

Fig. 47. Longitudinal section of an older fascicle of pine needles showing the absence of a fascicle sheath. P1143 E top X 14.

Fig. 48. Cross section of an older fascicle of pine needles showing the absence of a fascicle sheath. This section passed very near the base of the fascicle and would have included a fascicle sheath had one been present. P1143 D bot X 51.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Figs. 49 - 53. *Pinus* sp. (ms = microsporophyll, ps = pollen sac.)

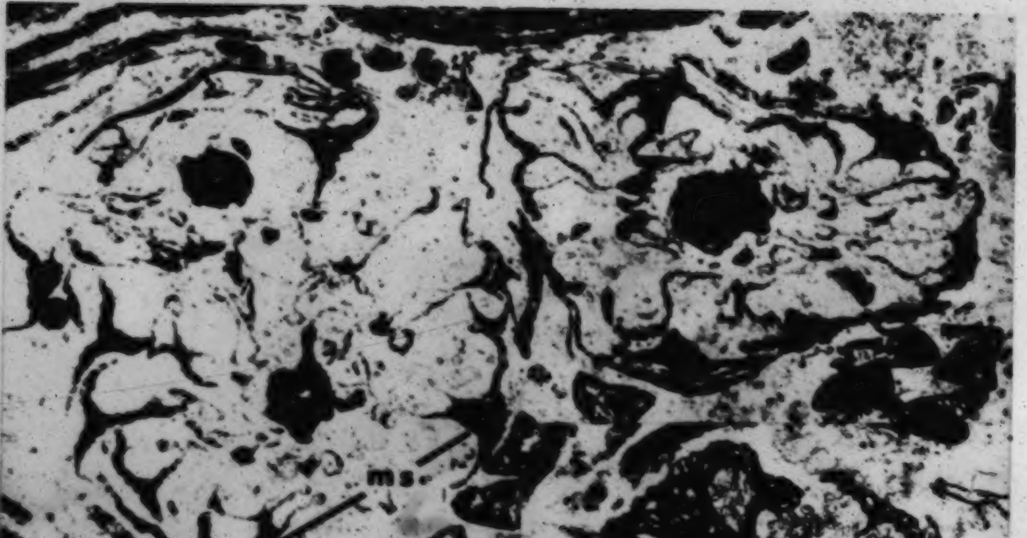
Fig. 49. Cross sections of three pollen cones. P1173 B bot X 20.

Fig. 50. Oblique longitudinal section of a pollen cone showing general features. Note the presence of two pollen sacs per microsporophyll. P1254 B bot X 24.

Fig. 51. Cross section of a pollen cone containing pollen grains. P1143 D bot X 40.

Fig. 52. Enlargement of the pollen sacs found in the specimen shown in Fig. 51. P1143 D bot X 90.

Fig. 53. Single pollen grain showing distinct corpus and sacci. P1143 D bot X 850.



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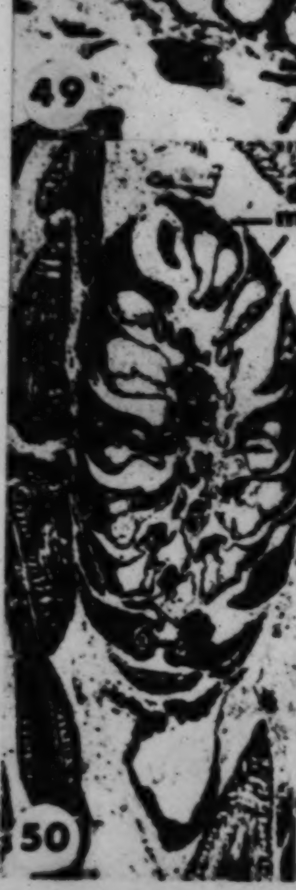

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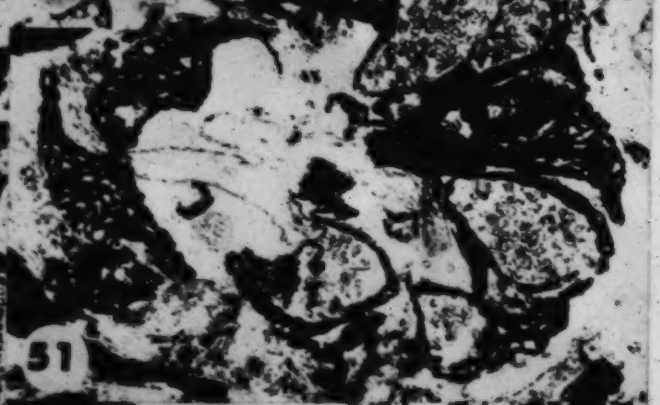

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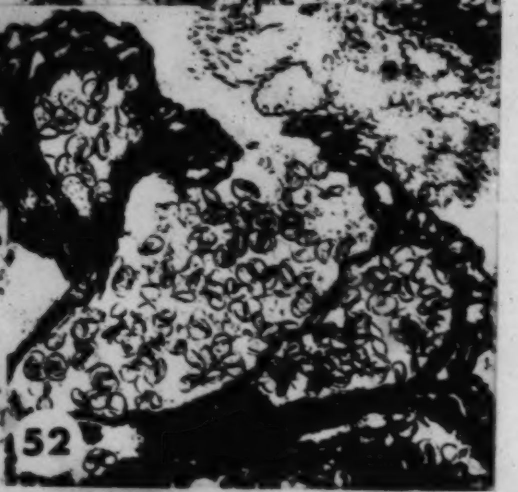

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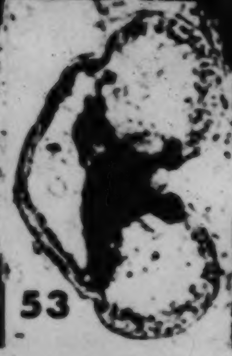

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Wood

DESCRIPTION - Taxodiaceous wood referable to this genus is common in the chert as fragments of very large stems, with imperceptible curvature of the annual-growth rings, and as intact twigs. In cross section (Fig. 58) the wood is seen to lack true resin ducts, although there are frequently rows of traumatic resin cysts. Prominent annual rings are formed by an abrupt change in tracheid size and lignification from spring to summer wood. Tracheids are angular in cross section and about 70 um at their greatest diameter.

Rays are uniseriate, with occasional paired cells in the body of the ray (Figs. 63, 66), and are very tall (Fig. 63). Up to 80 cells have been counted in some of the tallest rays. Ray tracheids have not been recognized. In the cross-field are 2 to 4 taxodioid pits (Fig. 60) with elliptical, oblique apertures.

Wood parenchyma is common (Fig. 59), and horizontal walls of these cells are smooth or what is described by Greguss (1955) as "indistinctly beadlike" (Fig. 66).

Circular bordered pits on the radial walls of the tracheids are uniseriate to triseriate and opposite (Fig. 59). The diameter of these pits, including the border, is approximately 20 um. Crassulae are discernible (Fig. 67), especially where paired pits occur. Smaller circular bordered pits may occur on the tangential walls of both early and late wood tracheids (Fig. 65). Tyloses are found in some tracheids (Fig. 62).

DISCUSSION - The identification of this wood as taxodioid rests primarily upon the anatomical descriptions of woods of the Coniferae by Greguss (1955). Although Greguss may be criticized for the vagueness of his keys and for the construction of his phylogenetic schemes, his descriptions are basically accurate. Caution should be used, however, in that Greguss usually had only fragments of the trunks of mature trees at hand, and any attempt at comparison with his material should be made using wood of a similar origin. Little is known of the differences among the woods of trunks, roots, and twigs and the use of wood from different organs may confuse assignments.

A distinctive feature of the Taxodiaceae which is found in the fossil is the presence of smooth tangential walls of the ray cells (Greguss, 1955). This feature, Greguss notes, is also found in the Podocarpaceae and Araucariaceae, but characteristics of the horizontal and radial walls of the ray cells and of cross-field pitting readily distinguish these two families from the Taxodiaceae. Other features of the Taxodiaceae that are present in the fossil are distinct growth rings and growth ring delimitations, angularity of the tracheids in cross section, absence of resin ducts except for occasional traumatic cysts, tall, uniseriate rays, wood parenchyma, absence of spiral thickenings in tracheids, up to 3 or 4 rows of opposite pits on the radial walls of tracheids, and taxodioid pitting in the cross-field.

The Taxodiaceae is divisible into two groups based on the nature of the horizontal walls of wood parenchyma, which are primarily dentate or beadlike in Glyptostrobus and Taxodium and smooth in Sequoia, Sequoiadendron, Metasequoia, Cryptomeria, Athrotaxis, Taiwania, and Cunninghamia. The fossil belongs to this latter assemblage, which can further be divided into two groups; the first containing Sequoia, Sequoiadendron, and Metasequoia, the second, the remaining four genera. This is done by Greguss (1955) on the thickness of the horizontal walls of ray parenchyma. Although true wall thicknesses are often obscured in fossilization, the fossil appears to belong to the former. In addition, there is a tendency for the formation of very tall rays found in the former. Within the Taxodiaceae, resin cysts tend to appear in the wood of Sequoia, Metasequoia, and Athrotaxis, whereas cysts were not found by Greguss in other members of the family.

Distinction among the woods of Sequoia, Sequoiadendron, and Metasequoia is difficult, but can be done using the following features:

1. Cross-field pits in Sequoia have large, almost circular apertures that nearly conform to the border. In Sequoiadendron, these pits have an elliptical aperture whose long axis is nearly horizontal. An elliptical aperture is found in Metasequoia as well, but the long axis is inclined at an oblique angle.
2. Circular bordered pits on the radial walls of tracheids

are smaller in Sequoia (14 - 16 um) and Sequoiadendron (14 - 17 um) than in Metasequoia (20 - 22 um). In both characteristics the fossil wood shows an affinity to Metasequoia. An additional characteristic noted for Metasequoia by Greguss, and found in the fossil, is distinct crassulae.

It becomes apparent that the fossil wood conforms in nearly every detail with the wood of Metasequoia glyptostroboides.

No ray tracheids have been recognized in the fossil wood, but this may be due to their scarcity, as they are not common in living Metasequoia, or to a failure of these thin-walled transverse tracheids to be adequately preserved.

The only obvious difference between the fossil and M. glyptostoboides is the much higher rays of the former. In this respect, the fossil is very similar to Taxodium distichum, where rays to 60 cells in height are found. If the ray height in the fossil is assumed to be representative of the species and not of an environmental origin, then ray height may indicate a relationship between extant species of Taxodium and the fossil. This will be discussed following the description of taxodioid leaves.

Leaves

DESCRIPTION - Small, coniferous leaves are found in association with both Metasequoia pollen cones and the wood described above. They occur in abundance but are rarely found to be well preserved and have not yet been found attached to twigs (Fig. 68).

The leaves are flat and measure 1.3 - 1.5 mm in width and about .35 mm in thickness. The length has not been ascertained. At the center of the leaf is a single vascular bundle which possesses a poorly defined parenchymatous bundle sheath (Fig. 71). A single mucilage duct is found on the abaxial side of the leaf between the vascular bundle and the lower epidermis. There is a notable absence of palisade mesophyll, the cortex of the leaf being comprised of large cells of an irregular shape and occasional transfusion cells (Fig. 71). A small bundle of heavily thickened fibers lies on the adaxial side of the vascular bundle and contacts the upper epidermis. Stomata have not been investigated.

Small twigs are found in association with the leaves (Fig. 68). Leaves have not been found attached to these shoots, but leaf bases on the twigs show structural similarity to the isolated leaves. Leaves are borne in a distichous manner on the shoots.

DISCUSSION - Ovoid or flattened leaves can be found in a number of conifers, but only in the Cupressaceae, Taxaceae (excluding Taxus), Cephalotaxaceae, Taxodiaceae, Podocarpaceae, and Tsuga of the Pinaceae are found just one mucilage or resin duct between the vein and the lower epidermis (Esau, 1960). Others such as Abies and Larix have typically two ducts, one on each side (left and right) of the vascular bundle.

In the Cupressaceae, only Juniperus has needle-like leaves, others having scale-leaves. Leaves of Juniperus are similar to the fossil leaves except that there is a distinct palisade layer on the adaxial side of the leaf. Tsuga, Podocarpus, and all genera of the Taxales show a well developed palisade layer and prominant bundle sheath.

A remarkable resemblance exists between the fossil leaves and leaves of Taxodium (Figs. 70 - 73). Other taxodioid genera such as Sequoia and Cunninghamia have a palisade layer, while Cunninghamia and Metasequoia typically have more than one mucilage duct.

Although the resemblance of the fossil leaves to leaves of Taxodium is marked, there is a close association of these fossil leaves with other remains assignable to Metasequoia. The distichous arrangement of leaf bases on associated vegetative shoots which are believed to have borne these leaves is also strong evidence for their referral to Metasequoia.

Since pollen cones, wood, and leaves have been found in close association with one another, and there is apparently only one type of each organ present, it is very probable that they all represent different organs of the same species. However, they show a combination of features of two modern genera: Pollen cones are like those of *Metasequoia*; wood is basically like that of *Metasequoia*, but shows some resemblance to *Taxodium*; and the leaves are most like those of *Taxodium*. Since these organs are considered to represent a single species, the fossil may provide information on the evolutionary relationships between *Taxodium* and *Metasequoia*.

Arnold and Lowther (1955), when reporting on their controversial genus *Parataxodium*, reviewed the history of *Sequoia*, *Metasequoia*, and *Taxodium*. It appears that *Sequoia* was first to become differentiated from a basic ancestral stock during the early Mesozoic. Two evolutionary lines resulted: one involving species such as *Sequoia jeholensis*, *S*. *affinis*, and *S*. *sempervirens*; the other, according to Arnold and Lowther, including species such as their *Parataxodium* *wigginsii*. From this latter group they suggest *Metasequoia* evolved during the Upper Cretaceous and *Taxodium* during the latest Cretaceous or early Tertiary.

In view of the possible evolution of *Metasequoia* followed shortly by *Taxodium* during the Upper Cretaceous, it is reasonable to expect that a complex of closely related plants including early forms of *Metasequoia* and *Taxodium* existed during the early Tertiary. These forms may not yet have evolved all the characteristics of their modern counterparts and may have had many primitive characteristics in common.

The species presented in this study appears to have been a part of this complex. Reproductively the fossil is apparently very close to Metasequoia glyptostroboides. Until seed cones can be found and examined, it will be uncertain as to the true reproductive relationships. Vegetatively, however, the fossil has not yet developed all of the characteristics of modern Metasequoia. The wood of the fossil has evolved basically the qualities of Metasequoia, although ray height is more like that of Taxodium. Leaves, however, are anatomically similar to those of Taxodium and have not developed characteristics of Metasequoia leaves. An important point of similarity between the fossil and Metasequoia is the arrangement of the leaves. Both the scale-like leaves of the pollen cones (Rothwell, 1975) and the leaves borne by the vegetative shoots are produced in a distichous manner which is a characteristic of Metasequoia.

It should be noted that basic differences between the leaves of both the fossil and Taxodium and those of Metasequoia are an increased number of mucilage ducts, a slight development of a palisade mesophyll, and a generally greater width. There is a tendency toward formation of a palisade layer in Taxodium and the fossil. Both the formation of palisade mesophyll and the increased number of mucilage ducts in Metasequoia may be a function of the much greater leaf size attained by Metasequoia. Only the very smallest Metasequoia leaves approach the size of the fossil leaves. However, even the smallest of Metasequoia leaves studied had three mucilage ducts throughout most of their length, whereas none of the fossil leaves were found to have more than one duct.

Despite some vegetative differences with Metasequoia glyptostroboides, the fossil species is here referred to the genus Metasequoia. Although close similarities are indicated, the true relationships of the fossil to M. glyptostroboides will be uncertain until further study of the vegetative remains is completed and seed cones have been found. Comparisons with other fossil species of Metasequoia must also await further investigation. However, the lack of preserved anatomical and reproductive detail in other fossil forms may not allow useful comparisons.

The combination of features found in the fossil implies a lesser degree of distinction between Taxodium and Metasequoia in the early Tertiary than may have been previously recognized. Morphologically Metasequoia is readily distinguishable from Taxodium in sediments of that age, but the fossil presented here reveals that anatomical differences are less pronounced. Since that time these forms have evolved into unique genera.

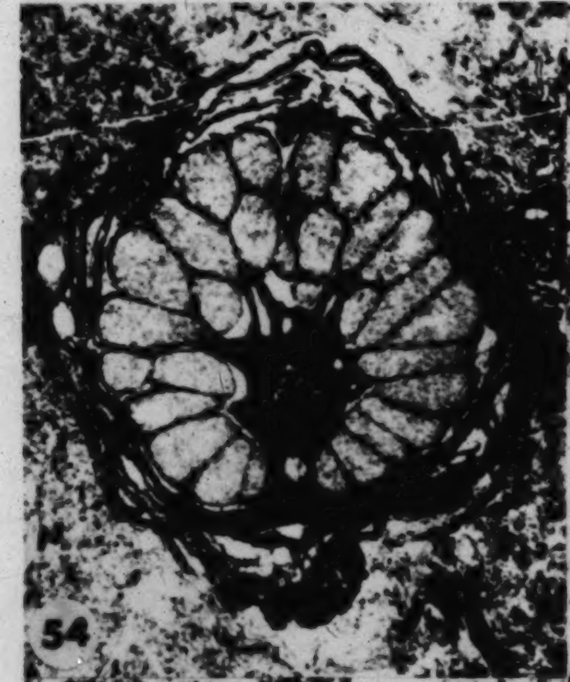
Figs. 54 - 57. *Metasequoia* sp. (md = mucilage duct, ms = microsporophyll).

Fig. 54. Cross section of a pollen cone showing general features. P1249 C top X 25.

Fig. 55. Cross section of a pollen cone showing the prominent mucilage duct present in each microsporophyll. P1195 E X 30.

Fig. 56. Oblique section of a pollen cone showing the attachment of three pollen sacs per microsporophyll (top). Note also the large mucilage duct in each microsporophyll. P1209 I top X 29.

Fig. 57. Pollen grains found in the specimen shown in Fig. 56. Note that the grains are spherical and papillate. P1209 I top X 265.



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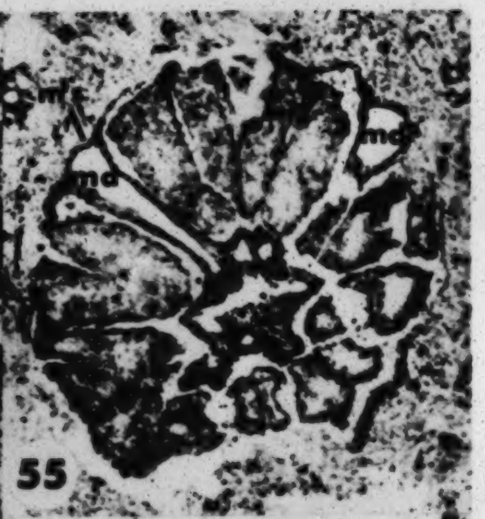

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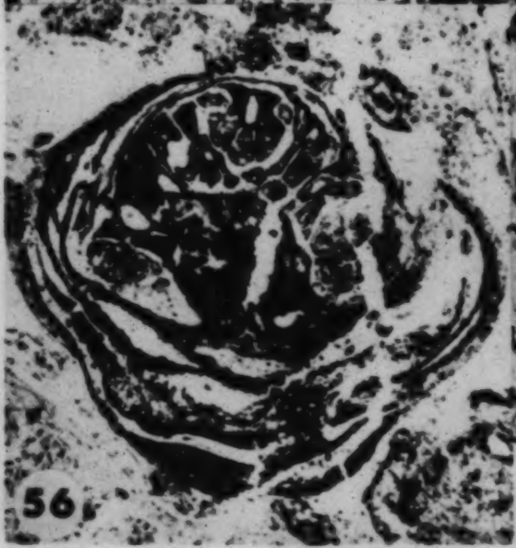

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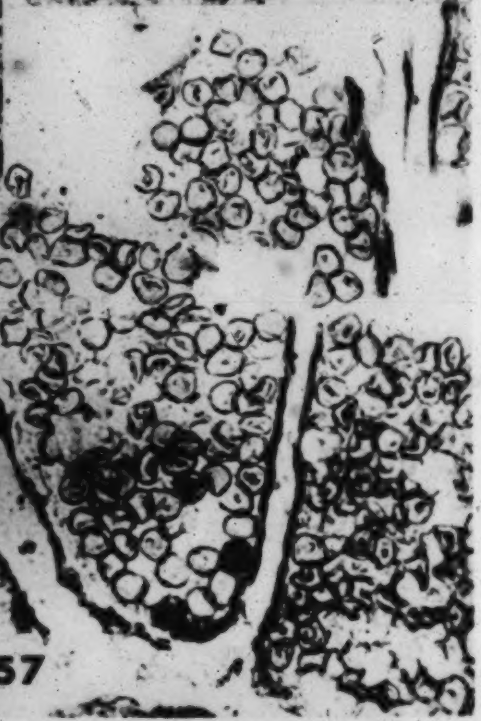

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Figs. 58 - 62. Metasequoia sp. Cross and radial sections of wood. (trc = traumatic resin cyst).

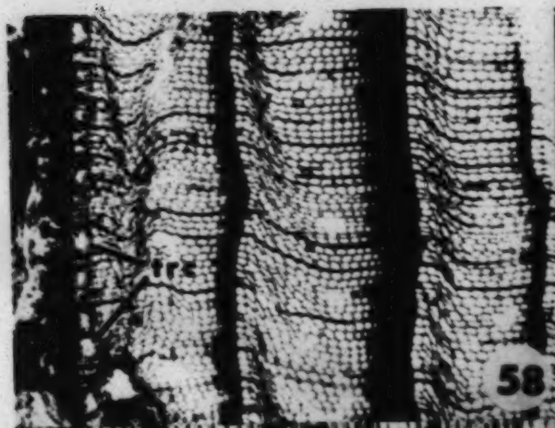
Fig. 58. Cross section showing the angularity of the tracheids and the abrupt change from early to late wood. Note the row of traumatic resin cysts in the early wood to the left. P1102 E X 29.

Fig. 59. Radial section of wood showing general features. Note the primarily bi- and triseriate, opposite pitting. P1102 E X 25.

Fig. 60. Radial section showing cross-field pitting. The pits appear as slits inclined at an oblique angle. P1102 E X 175.

Fig. 61. Traumatic resin cysts in radial view. P1102 E X 110.

Fig. 62. Radial section through several tracheids that have been occluded by what may be tyloses. P1102 E x 122.



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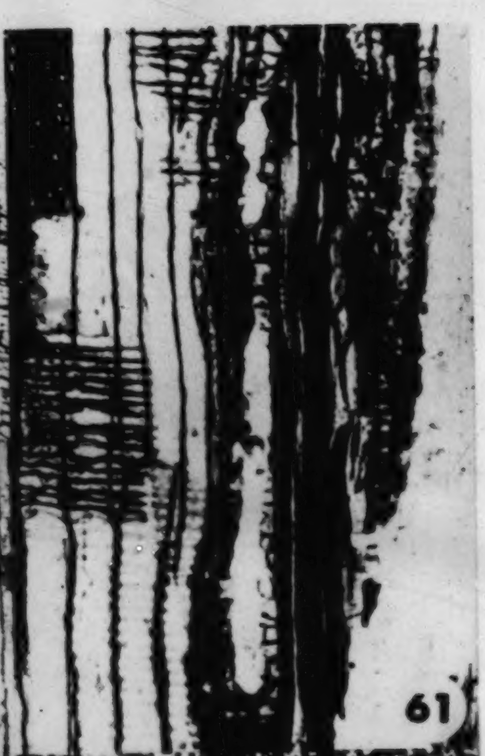

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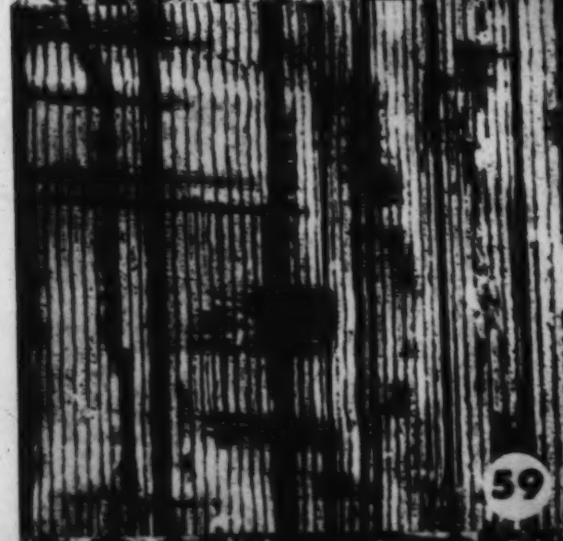

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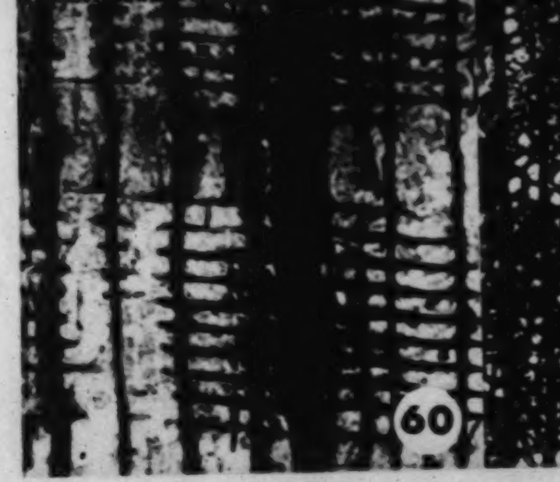

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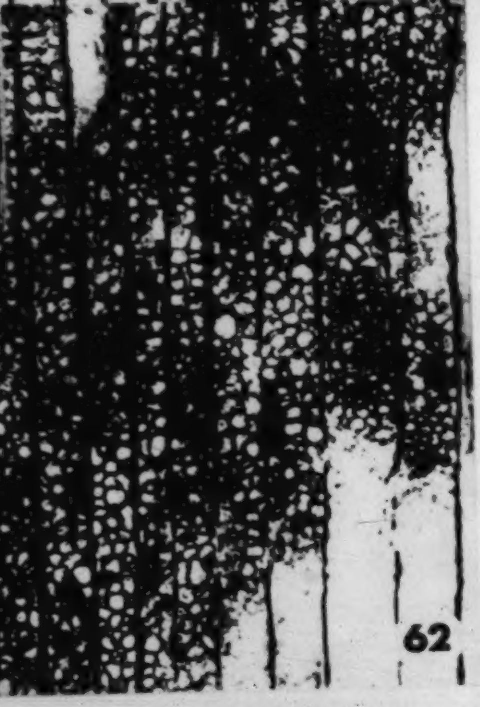

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Figs. 63 - 67. *Metasequoia* sp. Radial and tangential sections of wood. (cr = crassulae, tp = tangential pits).

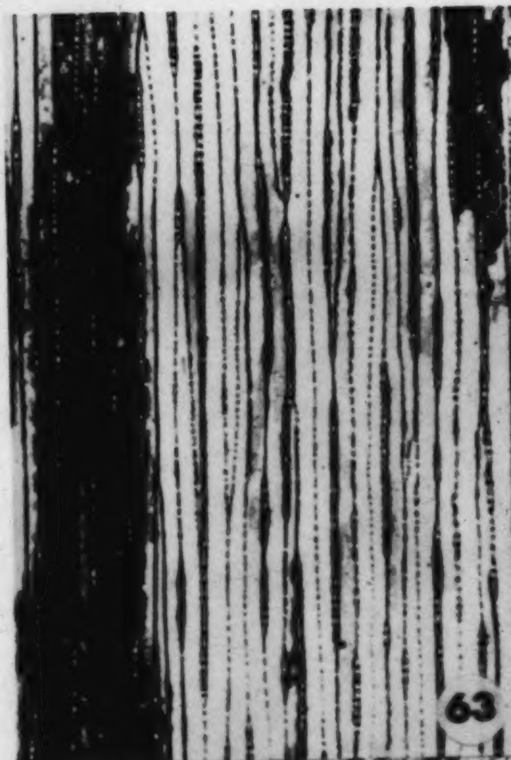
Fig. 63. Tangential section of wood showing general features. Note the variation in ray height from one to over 60 cells (the tall ray to the left is 80 cells high). P1102 E X 62.

Fig. 64. Tangential section showing wood parenchyma. Note the resinous contents of the cells. P1102 E X 62.

Fig. 65. Pitting on the tangential walls of the tracheids. P1102 E X 80.

Fig. 66. Closeup of the wood parenchyma cells shown in Fig. 64. Note the smooth to slightly beadlike horizontal walls. Note also the paired cells in the body of the ray at the lower left. P1102 E X 220.

Fig. 67. Radial section showing crassulae between pairs of pits. P1102 E X 380.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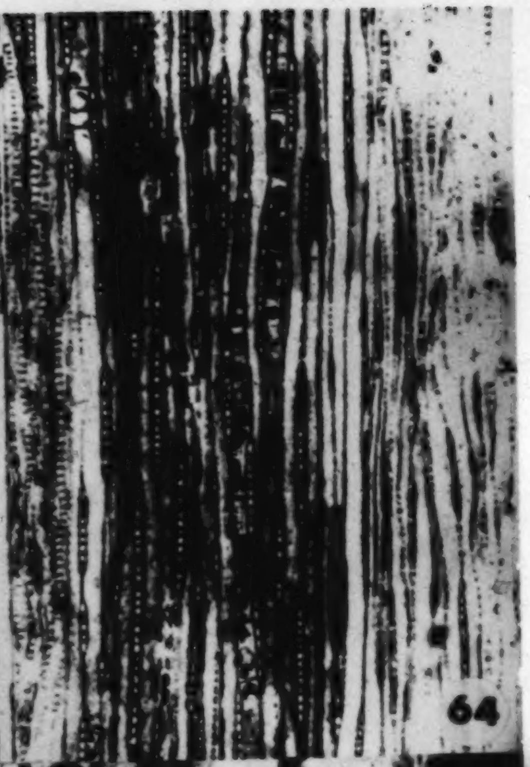
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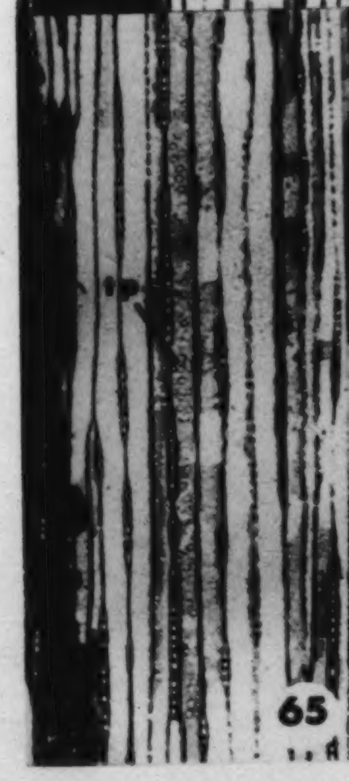
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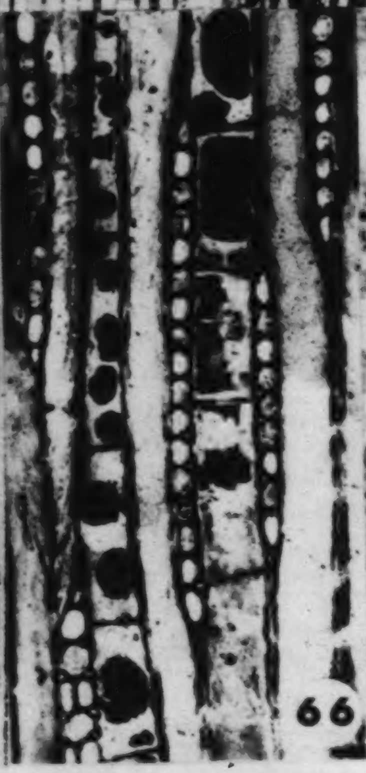
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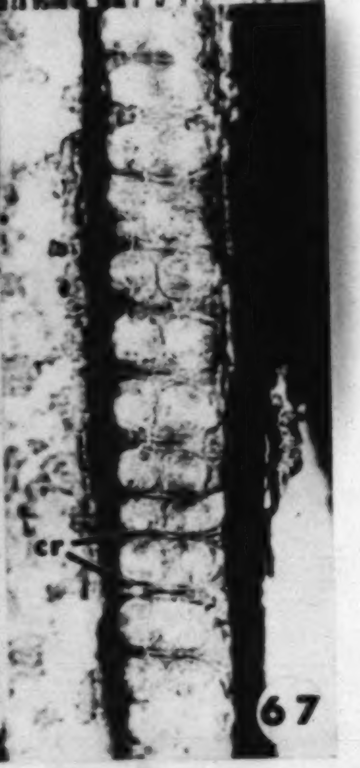
cr
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Fig. 68 - 73. Metasequoia sp. (lb = leaf base, md = mucilage duct, scl = sclerenchyma, tc = transfusion cell, x = xylem).

Fig. 68. Cross sections of a leaf and a small twig. Note the degree of structural similarity between the leaf and the leaf bases found on the shoot. Note also the opposite arrangement of leaf bases on the shoot. P1095 B bot X 55.

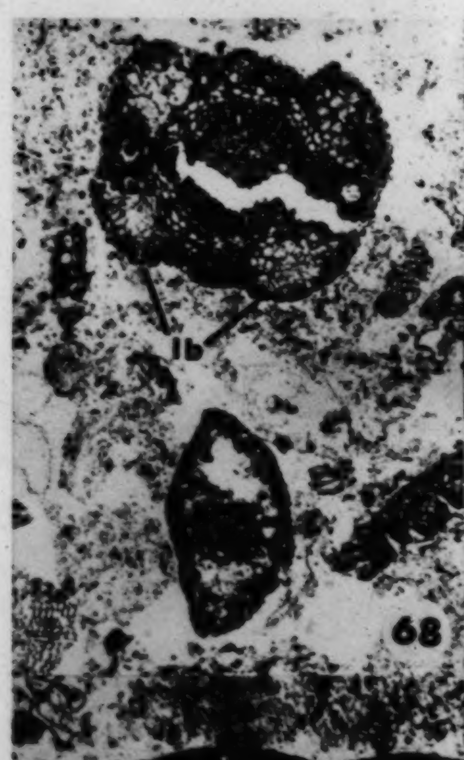
Fig. 69. Cross section of leaf showing general features. Note the single mucilage duct located between the vascular bundle and the lower epidermis. P1095 B top X 64.

Fig. 70. Cross section of a leaf. P1095 D top X 84.

Fig. 71. Closeup of the central portion of the leaf of Fig. 70. showing the vascular bundle mucilage duct, abaxial bundle of sclereids, and transfusion cells. P1095 D top X 180.

Fig. 72. Cross section of the leaf of Taxodium distichum. Compare with Fig. 70. X 106.

Fig. 73. Closeup of the portion of the leaf of Fig. 72. Compare with Fig. 71. X 235.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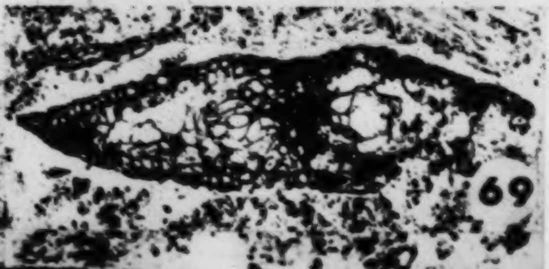
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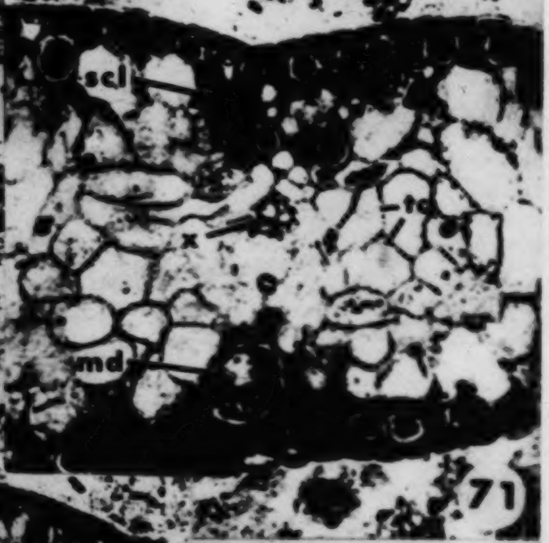
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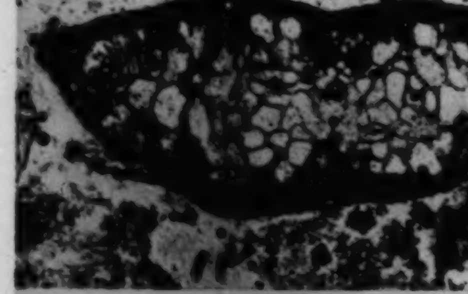
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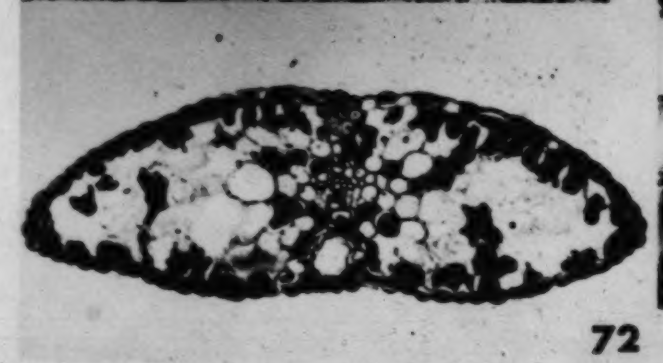
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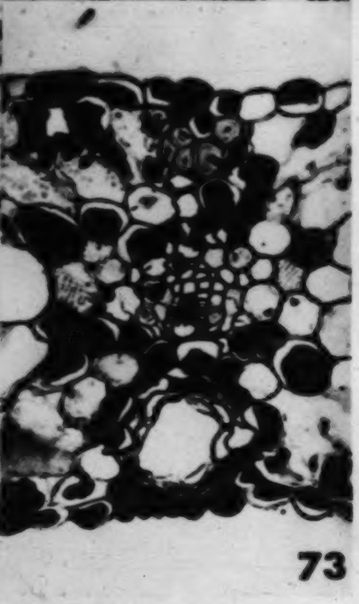
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Class: Angiospermae

Sub-Class: Dicotyledonae

Order: Rosales

Family: Rosaceae

Paleorosa similkameenensis, gen. et sp. nov. (Figs. 74-87)

Over 100 flowers assignable to this species were found scattered throughout several blocks of chert and in association with Pinus, Eorhiza, palms, and the remains of other angiosperms. Their discovery is of paramount importance in view of the rarity of identifiable flowers and other angiospermous reproductive organs in the fossil record and the resulting lack of knowledge of reproductive mechanisms of early angiosperms. There are some descriptions and reports of flowers as compressions found in the literature (Knowlton, 1917; Berry, 1913, 1916, 1930; MacGinitie, 1953; Becker, 1973; Krassilov, 1973; etc.), but their poor preservation rarely allows accurate identification. Recent work by Crepet, Dilcher, and Potter (1974, 1975) has, however, revealed remarkable details of some compressed flowers.

Some of the more spectacular fossil flowers have been found in the Oligocene, Baltic Amber. Extensive work has been done on these fossils (Goeppert and Menge, 1883; Conwentz, 1886; Czeczott, 1960), with many genera such as Quercus, Castanea, Acer, and Sambucus being recognized. Studies of other ambers (Hurd, Smith, and Durham, 1962;

Miranda, 1963; Langenheim, 1964; McAlpine and Martin, 1969) have revealed few flower parts.

Permineralized flowers have previously been found only in the Upper Cretaceous of Japan (Stopes, 1909, 1910; Stopes and Fujii, 1911) and in the Deccan Intertrappean series, Eocene in age, of India. Cretovarium japonicum was described from fragmentary remains by Stopes and Fujii as possibly liliaceous. Specimens of five species of petrified flowers have been described from the Mohgaon-Kalan beds of India. They are Sahnianthus parijai (Shukla, 1944; Chitaley, 1950, 1955), Sahnipushpam shuklai (Shukla, 1950; Verma, 1956; Parkash, 1956; Prakash and Jain, 1964; Chitaley, 1964), Chitaleypushpam mohgaoense (Paradkar, 1973), Deccananthus savitrii (Chitaley and Kate, 1974), and Raoanthus intertrappea (Chitaley and Patel, 1975). Unfortunately, accurate reconstructions of these flowers have not been made and affinities are uncertain.

The flowers described here are by far the best preserved and most completely understood of all permineralized flowers known to date. Superb preservation, rarely possible for soft floral parts, has permitted reconstruction and made it possible to identify the fossils as members of the family Rosaceae. These fossil flowers, which are the oldest known rosaceous flowers, have provided valuable information on early floral evolution in this family.

Basically two different stages of floral development are seen. One is found as a somewhat immature form, where the flowers appear to be buds (Figs. 76,77,78,84); the other, a slightly larger, more mature form (Figs. 75,81,83) has young seeds but lacks petals and stamens. On considering similarities in structure and studying two specimens which possessed both young seeds and stamens (Fig. 83), it was concluded that these two types represent different developmental stages of a single species. Preservation is often less complete in the immature form. The presence of a variety of developmental forms, all found detached from the parent plant, could be the result of trauma experienced during the influx of hot, mineral rich water prior to permineralization. This can also account for the lack of later stages of fruit development, for only those stages borne by the dying plant would be available for fossilization.

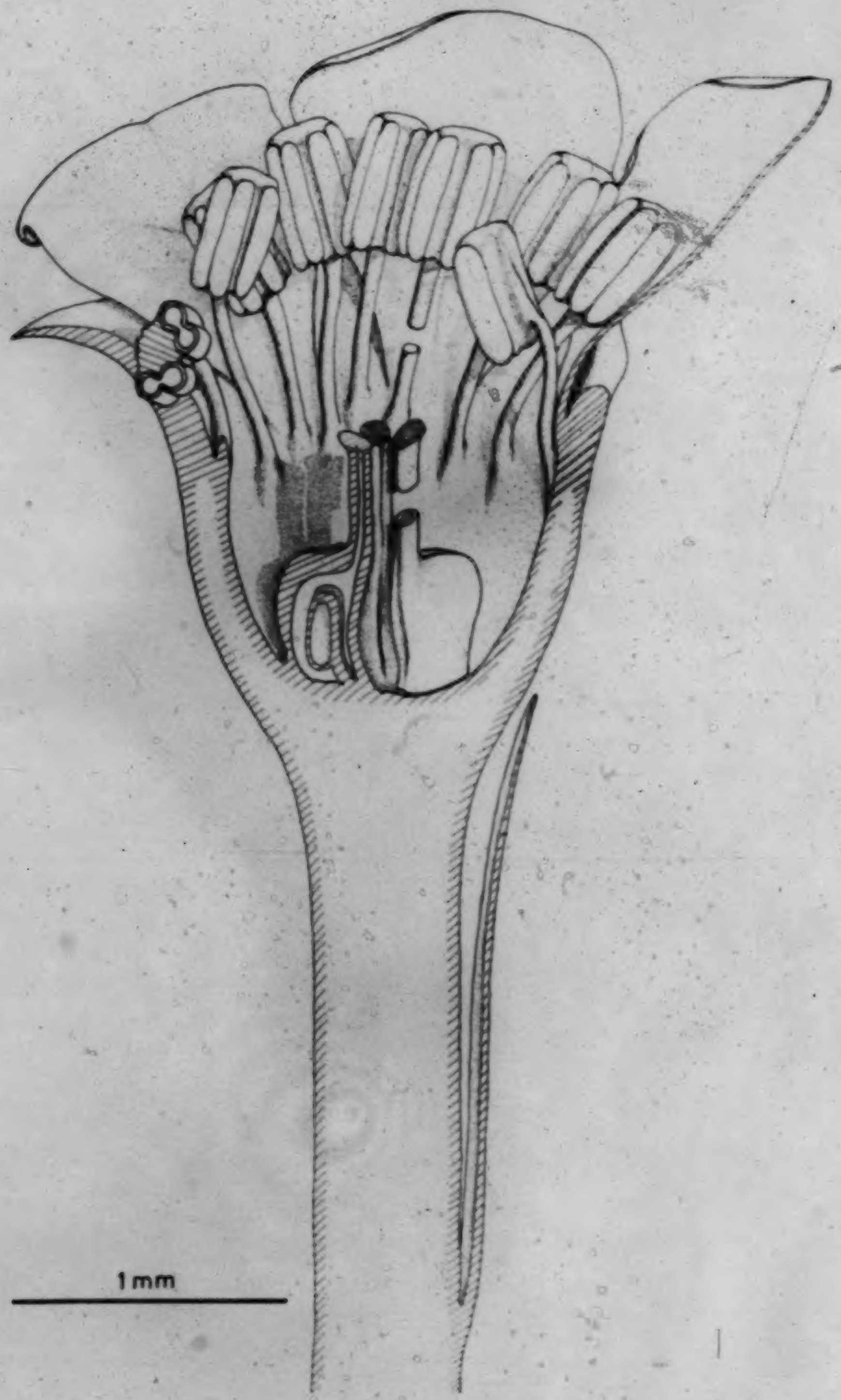
Each flower (Fig. 74) is borne on a pedicel to which is attached a single bract. A striking feature is the floral cup which is comprised of the fused bases of the sepals, petals, and stamens. The flowers are pentamerous, with alternate insertion of the sepals and petals. Stamens are indefinite in number, varying from 13 to 19. The five carpels are free and each contains two erect ovules. The complete perianth and included stamens suggest entomophilly.

SYSTEMATIC DESCRIPTION:

Generic diagnosis: Paleorosa gen. nov.

Flowers permineralized, bisexual, actinomorphic. Five sepals and five petals inserted alternately, many

Fig. 74. Reconstruction of Paleorosa similkameenensis showing a median longitudinal section of the flower. Hairs that cover carpels and styles have been omitted. For further explanation of details see text.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stamens, five free carpels. Floral cup surrounding apocarpous gynoecium. Ovules 2 per carpel, collateral, basally attached, erect, and anatropous. Fruit, mature seeds, and vegetative structures unknown.

Type species: Paleorosa similkameenensis sp. nov.

Flowers as described in generic diagnosis. Pedicel 1.2 - 1.7 mm long, 0.4 - 0.5 mm in diameter, with single bract 1.0 - 1.6 mm long attached at base. Floral cup 0.5 - 1.8 mm in diameter, 0.5 - 1.4 mm deep from point of insertion of petals to base of cup. Sepals 0.5 - 0.8 mm long. Size of petals unknown. Number of stamens variable, 13 - 19, filaments 0.3 - 0.4 mm long, 0.1 mm in diameter. Anthers bilocular, dorsifixed, 0.5 - 0.6 mm high, 0.2 - 0.4 mm wide. Carpels pubescent, inserted opposite sepals, borne at base of floral cup, fused to wall of cup up to level of ovular insertion, free at ventral margins. At stages of early seed development, carpels 0.7 - 1.1 mm high, 0.4 - 0.5 mm wide, 0.4 - 0.5 mm deep. Style terminal, 1.1 - 1.3 mm long, 0.2 mm in diameter, with hollow center. Dorsal vascular bundle of carpel continues into style. Ovules 0.5 - 0.9 mm long, 0.2 mm in diameter basally attached, erect on funiculus 0.1 mm long, anatropous.

Holotype:

University of Alberta Paleobotanical Collection (UAPC) chert block No. P1122I. Cross section from which serial sections were made. Slides Nos. 2545-2550. Fig. 75.

Paratypes:

UAPC No. P1118E bot. Longitudinal section, slides Nos. 2555-2556. Figs. 77,87. UAPC No. P1119J bot. Oblique longitudinal section, slides Nos. 2543-2544. Figs. 80, 84. UAPC No. P1123B top. Longitudinal section, slides Nos. 2551-2554. Fig. 76. UAPC No. 1143E bot. Oblique cross section, slides Nos. 2557-2580. Figs. 81, 82, 85.

Type Locality:

On the east bank of the Similkameen River, 8.4 kilometers SSW of Princeton, British Columbia. Allenby Formation, Middle Eocene.

Derivation of Name:

Paleo, Latin for ancient; rosa, rose. Specific epithet from type locality on Similkameen River.

DESCRIPTION - The pedicel is rather short and has a single, small bract of about equal length attached to its base (Fig. 76).

Lower portions of the sepals, petals, and stamens are fused to form a floral cup 0.5 - 1.8 mm in diameter and 0.5 - 1.4 mm high (Figs. 73,77). Sepals appear to be continuous with the floral cup, which thus resembles a five-lobed calyx tube. Petals and sepals are inserted alternately. Since only the flowers in bud possessed petals, dimensions of the petals could not be accurately measured. However, their length is estimated at 1.5 mm, with a width of about the same. The floral cup is vascularized by ten major bundles (Fig. 75) reflecting the pentamerous structure of Paleorosa. The quality of preservation in this part of the flower did not permit a study of the vascularization of sepals and petals. The wide range in measurements of floral parts is, to a large part, due to the different developmental stages of the flowers. Measurements approximately midway between the extremes would most nearly represent dimensions of a flower at anthesis.

Stamens consist of rather large (0.5 x 0.3 mm) anthers and short (0.4mm) filaments (Fig. 77,79). The anthers were apparently not elevated far beyond the perianth, are dorsifixed, and possess a broad connective. Figure 87 shows the discontinuity of the septum between adjacent pollen sacs, forming a bilocular condition. Stamens are of a variable number. Counts from flowers in bud, from which no stamens could have been lost, vary from 13 to 19. A few of the anthers contain the remains of pollen grains (Figs. 77,79,87). These pollen grains are not well preserved and may have been immature at the time of permineralization. However, Boneham (1968) was able to recover very little dispersed pollen from the layers of chert and what he did find was poorly preserved. Physical factors at the time of fossilization, therefore, may have inhibited the preservation of pollen grains.

Five pubescent carpels are inserted at the base of the floral cup, opposite the sepals. A single specimen, which is similar to the rest of the flowers in all other respects, has six carpels and presumably reflects variability within the species. The carpels are free from one another, but are fused to the floral cup up to the level of ovular insertion (Fig. 75). Often the ventral margins of adjacent carpels appear fused (Fig. 75), but a close examination reveals a continuous epidermis surrounding each carpel. In the central region there appears to be some type of material, but it is not certain whether it is detrital, is made up of a mat of hairs, or is a raised torus, since no cellular detail has been preserved.

Each of the five carpels is supplied by a dorsal vascular bundle, two ventral or wing bundles, and a number of vegetative bundles (Fig. 81). Only the dorsal bundle continues into the style. Although a vascular strand is cearly visible in the funiculus, it was not possible to see the origin of the ovular supply.

The styles extend to the upper level of the floral cup (Figs. 83,84) and, in cross section, are hollow with a dorsal bundle and a well defined ventral suture (Fig. 86). This suture is evident in both the style and the carpel body (Fig. 82). Although not well preserved, the stigmatic surfaces appear to have been simple.

Ovules are two per carpel, basally attached, erect, and anatropous. The two integuments (Fig. 82) are interpreted as free, for they are sometimes separate from one another. Flowers that show structural preservation of the carpels are in a post-fertilization state of development, but have not yet undergone fruit formation. Although there is some tissue preserved in several of the developing seeds, embryos have not been recognized. Considering the state of maturation of these flowers, this tissue may represent endosperm.

Each carpel contains ovules which appear equally well developed, and likely formed a two-seeded follicle.

DISCUSSION - A floral cup can be found in a large number of families and can be broadly interpreted as a fusion of basal portions of sepals, petals, and stamens (van Tieghem, 1875; Eames, 1931; Jackson, 1934; Wilson and Just, 1939; MacDaniels, 1940; Cronquist, 1968). It was once widely believed that the floral cup was not appendicular but receptacular in origin (Prayer, 1857; Rydberg, 1898; Krause, 1913, Judson, 1929, etc.). Receptacular floral cups, however, are now considered to be the case in only a few families such as the Eupomatiaceae (Magnoliales), Calycanthaceae (Laurales), Santalaceae (Santales), and perhaps Cactaceae (Caryophyllales) (Boke, 1964; Cronquist, 1968). In the Rosaceae, the genus Rosa has been shown to possess a floral cup that is in part both appendicular and receptacular (van Tieghem, 1878; Bonne, 1928; Jackson, 1934). Though detailed study of the vasculature is necessary in order to determine the type of origin, a cup formed of a hollowed receptacle is the less common condition and is often characterized by having carpels borne on the walls of the cup. Since there is apparently no carpellary component, the floral cup of Paleorosa is interpreted as appendicular.

Families containing members with floral cups that could be considered similar to those of this fossil include: Lauraceae, Monimiaceae (Laurales); Aristolochiaceae (Aristolochiales); Hamamelidaceae (Hamamelidales); Ebenaceae, Styrocaceae (Ebenales); Loasaceae (Violales), Moringaceae (Capparales); Rosaceae, Saxifragaceae (Rosales); Myrtaceae, Lythraceae, Onagraceae, Melastomataceae (Myrtales); Staphyllaceae (Sapindales); Celastraceae (Celastrales); Rhamnaceae, Vitaceae (Rhamnales); and Caryophyllaceae (Caryophyllales).

Many wholly epigynous families have not been included because they are generally considered rather advanced and have evolved from families which possess members with superior gynoecia. Formation of a floral cup and the resulting condition of perigyny have been interpreted as a step toward epigyny where the carpels and floral cup have fused (Cronquist, 1968). Epigyny, however, is not necessarily dependent upon ancestral perigyny, but may arise through adnation of free floral parts to the carpels. This may have occurred in families such as the Rubiaceae and Campanulaceae, for Cronquist (1968) states that in these two families "... there is no history of a separate hypanthium.".

In nearly all families listed above, the development of a syncarpous gynoecium preceded the development of a floral cup. Only a few families such as the Rosaceae, Saxifragaceae, and Monimiaceae have members with both an apocarpous gynoecium and a floral cup. Of these, only in the Rosaceae are found all other features of the fossil: pentamerous and actinomorphic perianth, numerous stamens of an indefinite number, five free carpels, and two ovules per carpel.

Although the genera of the Rosaceae have been isolated in smaller families (Payer, 1857; Bessey, 1915; etc.), the Rosaceae has been recognized as a very natural group by the majority of taxonomists (Lawrence, 1951; Hutchinson, 1973; Robertson, 1974; etc.). In such a closely knit family, however, tribal limits are more difficult to deal with. The Rosaceae has been variously divided into sub-families and tribes by such authors as de Candolle (1825), Bentham and Hooker (1865), Focke (1894), Rydberg (1908), Schulze-Menz (1964), and Hutchinson (1964). The most recent classification has been prepared by Robertson (1974), whose system of four sub-families and 15 to 17 tribes is the system used here. Robertson discusses the treatment of the genus Holidiscus, but does not give it a definite position. This genus is considered here as belonging to a distinct tribe, the Holodisceae, of the sub-family Spiraeoideae (Focke, 1894; Schulze-Menz, 1964). The sub-family Maloideae is considered as consisting of a single tribe and ~~is~~ not split into the tribes Crataegeae and Sorbeae, a division which Robertson (1974) says, "... may not best reflect generic relationships.".

Within the Rosaceae, tribes which include members with five carpels and two ovules per carpel are the Osmaronieae (Amygdaloideae), Maleae (Maloideae), Spiraeeae, Holodisceae, Quillajeae, Sorbarieae (Spiraeoideae), and Ulmarieae (Rosoideae). A difficulty arises in attempting to immediately assign Paleorosa to one of these tribes, since it is the nature of the fruit that basically determines affinities. With the exception of the Osmaronieae, which appears to be highly modified, any of these tribes might accommodate Paleorosa, since its fruit is unknown.

From a phylogenetic point of view, the Rosaceae is a very important family. It is believed that families such as the Saxifragaceae, Leguminosae and, indeed, all families of the Rosales find their origin directly or indirectly in the Rosaceae (Cronquist, 1968). Furthermore, all orders of the sub-class Rosidae can be traced to the Rosales (Bessey, 1897, 1915; Cronquist, 1968). The sub-class Asteridae may be derived from certain members of the Rosidae (Bessey, 1897, 1915; Cronquist, 1968; Takhtajan, 1969). The Rosidae contains more than one-third of all species of dicotyledons. The origin of this very prolific group of angiosperms appears to lie within the Rosaceae, and the necessity of understanding evolution within this family is clear. Paleorosa represents one of the oldest fossil members of this family, and is the oldest known fossil flower that can be positively identified as rosaceous.

Spiraeoid tribes are considered ancestral within this family, but opinions vary as to the nature of the ancestral type. It has been proposed that the many-seeded follicle of most spiraeoids was derived from an ancestor within the Dilleniaceae or a similar family (Bailey and Swamy, 1951; Eames, 1961; Hutchinson, 1964), although the sub-classes Dilleniidae and Rosidae have been considered as parallel lineages with their origins in the Magnoliidae (Cronquist, 1968). A more recent theory holds that the primitive rosaceous carpel has but two seeds and represents an independent line of evolution with its origin in the Magnoliales (Sterling, 1964c, 1966a, c). Although Sterling (1969) and Eyde (1975) have found evidence for a reduction from many- to few-seeded carpels among extant, multiovulate spiraeoids, a biovulate condition is found in members of the Quillajeae and Sorbarieae which are most closely alligned with magnoliaceous groups (Sterling, 1966c).

Studies of rosaceous floral anatomy by such authors as Maximowicz (1879), Juel (1918, 1927), Bonne (1928), and Sterling (1964a, b, c, 1965a, b, c, 1966a, b, c) have contributed to a better understanding of relationships within the family. Some of the evolutionary trends proposed for the Rosaceae are an increase or decrease in the basic numbers of five carpels and two ovules per carpel, fusion of the two integuments, intercarpellary fusion, carpel to floral cup fusion, and fusion of wing and ovular vascular bundles to reduce the carpellary supply from five to three major bundles.

The most primitive members of the family according to these criteria are to be found within the tribes Quillajeae and Sorbarieae. Although floral structure is similar in both tribes, the Quillajeae is considered the more primitive of the two on the basis of vegetative features and a tropical distribution (Hutchinson, 1964). Sterling (1966c) has pointed out, however, that in neither the Quillajeae, nor in any other tribe, is there found a species which combines all of the primitive features. All have become advanced in one or more ways.

Sterling (1966b, c) and Cronquist (1968) have noted that the position of the ovules may be important in determining relationships within the Rosaceae. In all of the Maloideae, ovules are basally attached, erect, anatropous, and apotropous (micropyle directed toward base of locule). In all other tribes, with few exceptions, ovules are apically attached, pendulous, anatropous, and epitropic (micropyle directed toward apex of locule), or can be derived from this condition (e.g., Dryadeae have erect ovules, but a basally inserted style). These exceptions are notably found in Quillaja and Vauquelinia of the Quillajeae and Gillenia and Spiraeanthus of the Sorbarieae.

Chromosome numbers also support recognition of the Maloideae as a distinct line. Base chromosome numbers of the Rosoideae are 7, 8, and 9; the Spiraeoideae, 8, 9, and

10; the Amygdaloideae, 8; and the Maloideae, 17 (Robertson, 1974). The only exception to these rules is a base number of 17 for Quillaja brasiliensis (Bolkhovskikh et al., 1969).

The possible relationships between the Quillajeae and Sorbarieae and the Maloideae have been discussed by van Tieghem (1875), Maximowicz (1879), Juel (1918, 1927), Bonne (1928), and Sterling (1966c). Differences are basically in the nature of the fruit, which is pomoid in the Maloideae and follicular in the Quillajeae and Sorbarieae. Chemotaxonomic evidence is also in agreement with relationships among these tribes (Challice, 1974).

The evidence presented suggests that there are two major lines of evolution within the Rosaceae. Both appear to have their origins within the Quillajeae and Sorbarieae, with one line deriving the Maloideae, the other, the bulk of the other three sub-families. Ovular position appears to be a fairly accurate indicator of affinities.

Thus, considering current views of the evolutionary trends in the Rosaceae, Paleorosa appears primitive in all observable features. Carpels are five (rarely 6) and free, ovules are two per carpel, integuments are two and apparently not fused, there is no intercarpellary fusion, and fusion of the carpels to the floral cup is minimal.

Sterling (1966c) notes that fusion of the ventral margins of adjacent carpels, without similar fusion of the carpels to the floral cup, is generally the trend in higher spiraeoids. Retention of free ventral margins of adjacent carpels, with progressive fusion of the carpels to the floral cup, is a trend found in the Maloideae. There is enough fusion of the carpels to the floral cup in *Paleorosa* to suggest a relationship with the Maloideae.

Paleorosa also has basally attached, erect ovules, which further supports its alliance with the Maloideae. Considering the slight degree of fusion (up to ovular insertion), however, it is unlikely that the fruit could have been a pome. It is more likely that the fruits were follicular as in the Quillajeae or Sorbarieae. Until fruits are found, a decision as to where *Paleorosa* fits among the groups must be made utilizing data from the living members that show comparable floral structure.

Flowers with similar features are found in *Pyracantha* of the Maloideae, *Vauquelinia* of the Quillajeae, and *Gillenia trifoliata* and *Spiraeanthus* of the Sorbarieae. However, as noted earlier all are modified in one or more ways. *Paleorosa* has less fusion of its carpels to the floral cup than does *Pyracantha*, which is possibly the least advanced member of the Maloideae. In *Vauquelinia* there is considerable intercarpellary fusion. *Spiraeanthus* has also undergone intercarpellary fusion and has ovules with single integuments. *Gillenia trifoliata* is possibly least modified, with some fusion of ventral carpellary margins, but lacking carpel to cup fusion. The situation is reversed in *Paleorosa*. Only those genera with erect ovules have been discussed. However, spiraeoids with pendulous ovules show similar structural modification.

An advanced character that is found in all Quillajeae and Sorbarieae, but which could not be determined in the fossil, is the fusion of ovular and wing vascular bundles to form a true ventral bundle (Sterling, 1966c). A vascular supply of five bundles (one dorsal, two wing, two ovular) to each carpel is the primitive condition among members of the Rosaceae (Sterling, 1953, 1964c 1966a, 1969; Cronquist, 1968). The three bundle condition found in most members of the Rosaceae has arisen secondarily by fusion of the ovular bundles to the wing bundles. This is unlike a primitive three bundle condition found in most other groups. It is unfortunate that the ovular bundles could not be traced into the receptacle, for the presence or absence of their fusion to wing bundles could strengthen the position of Paleorosa relative to the Quillajeae and Sorbarieae. The features described above for modern genera are summarized in Table 2 for comparison with those of Paleorosa.

It is apparent that all extant genera have been subject to some change and that the ancestor or "primitive type" is no longer living. The great similarity of floral structure among the more primitive genera with erect ovules and those with pendulous ovules within the Quillajeae and Sorbarieae suggests that this divergence, which distinctly divides the Rosaceae, occurred within the earliest members of the Rosaceae. It is not yet known which form the ancestor of the family would have had. Both erect and pendulous, paired

Table 2. Selected reproductive features of genera of the tribes Maleae, Spiraeeae, Holodisceae, Ulmarieae, Quilajeae, and Sorbarieae. (Information derived from Sterling, 1964a,b,c, 1965a,b,c, 1966a,b,c) Genera appear in the order by which they are treated by Sterling.

[1]Ovular insertion

a - apical
b - basal
pl - many ovules

[2]Integumentary fusion

+ fused
- free
+(-) most species fused
-(+) most species free

[3]Intercarpellary fusion

+ carpels fused above level of ovular insertion
(+) carpels slightly fused
- carpels free
0 single carpel involved

[4]Carpel to floral cup fusion

fraction of height through which carpels are fused to the floral cup
+ fusion to level of ovular insertion
(+) slight fusion
- carpels free from floral cup

	Ovular Insertion[1]	Number of Carpels	Number of ovules per carpel	Integumentary Fusion[2]	Intercarpellary Fusion[3]	Carpel to Floral Cup Fusion[4]
Maloideae						
Maleae						
Crataegus	b	1-5	2	+-	+-	.5-1.0+
Hesperomeles	b	5	1	+-	+	.7-1.0+
Mespilus	b	5	2	+	+	1.0
Osteomeles	b	5	1	-(+)	+	1.0
Chamaemeles	b	1	2	+	0	.9
Cotoneaster	b	2-3	2	-	-	.5- .8
Dichotomanthes	b	1	2	-	0	0 or less
Pyracantha	b	5	2	+-	-	.3- .5
Amelanchier	b	2-5	1-2	-(+)	+	.4-1.0
Aronia	b	5	2	+-	+	.5- .8
Malacomeles	b	2-3	1	+-	-	.6- .9
Malus	b	3-5	2	-	+(-)	1.0+
Peraphyllum	b	2-3	2	-	-	1.0+
Pyrus	b	2.5	2	-	+-	.8-1.0+
Sorbus	b	3	2	+-	-	.6- .9
Photinia	b	1-3	2	+-	+	.3- .8
Heteromeles	b	2	2	-	-	.4
Eriobotrya	b	2	2	+-	+	.6-1.0+
Pourthiaea	b	2-3	2	+-	+	.5- .7
Raphiolepis	b	2	2-4	+	+	1.0+
Stranvaesia	b	5	2	+-	+	.7- .9
Chaenomeles	pl	4-5	16-36	+(-)	+	1.0+
Cydonia	pl	5	15-48	-	+-	1.0+
Docynia	pl,b	5-7	4-7	-	-	.6- .8

	Ovular Insertion[1]	Number of Carpels	Number of ovules per carpel	Integumentary Fusion[2]	Intercarpellary Fusion[3]	Carpel to Floral Cup Fusion[4]
Spiraeoideae						
Spiraeae						
Aruncus	a	3	3-7	+(-)	(+)	-
Kelseya	a	3-4	3-7	+	-	+
Luetkea	a	5	3-7	+	(+)	-
Petrophytum	a	5	2	+	(+)	-
Sibiraea	a	5	3-7	+	-	-
Spiraea	a	5	sev	+	(+)	-
Holodisceae						
Holodiscus	a	5-6	2	+	-(+)	-
Ulmarieae						
Ulmaria Filipendula	a	5	2	+	(+)	-
Quillajeae						
Exochorda	a	5	2	-	+	+
Lindleya	a	5	2	-	+	+
Quillaja	b	5	10-16	-	+	-(+)
Kageneckia	a,b	5	14-20	-	-	-
Vauquelinia	b	5	2	-(+)	+	+
Sorbarieae						
Chamaebatiaria	a	5	sev	-	+	+
Lyonothamnus	a,pl	2	4-6	-	(+)	+
Sorbaria	a	5	sev	+-	+	+
Gillenia	b,pl	5	2,sev	-	(+)	-
Spiraeanthus	b	4-5	2	+	+	+
Paleorosa	b	5	2	-	-	+

ovules are found in magnoliaceous and annonaceous genera (Hutchinson, 1964).

Paleorosa seems to combine more primitive features than any living member of the Rosaceae. It probably represents an early group of rosaceous plants that preceded the Quillajeae and Sorbarieae, and may signify the incipient development of the Maloideae.

Rosaceous leaf remains appear frequently in the late Tertiary but are much less common in sediments older than Eocene (Kirchheimer, 1942). However, the accurate identification of many angiospermous fossils, particularly Cretaceous and early Tertiary leaves, is now being questioned (Dilcher, 1974). Remains of leaves and seeds assignable to genera such as _Amygdalus_ and _Prunus_ from the Upper Cretaceous and Eocene may support the theory that the _Amygdaliodeae_ was one of the earliest rosaceous lines to emerge (Sterling, 1966b; Robertson, 1974). Remains attributable to the other three sub-families are apparently scarce in sediments older than Oligocene. _Paleorosa_ is one of the oldest known members of the Rosaceae, and is presently the oldest known rosaceous flower. Thus, it is the earliest well documented record of rosaceous floral structure. If _Paleorosa_ is an accurate indicator of the state of floral development in the Rosaceae during the Middle Eocene, then this is evidence that supports the theory, mainly derived from floral anatomy of living representatives, that the tribes Quillajeae and Sorbarieae are, indeed, primitive.

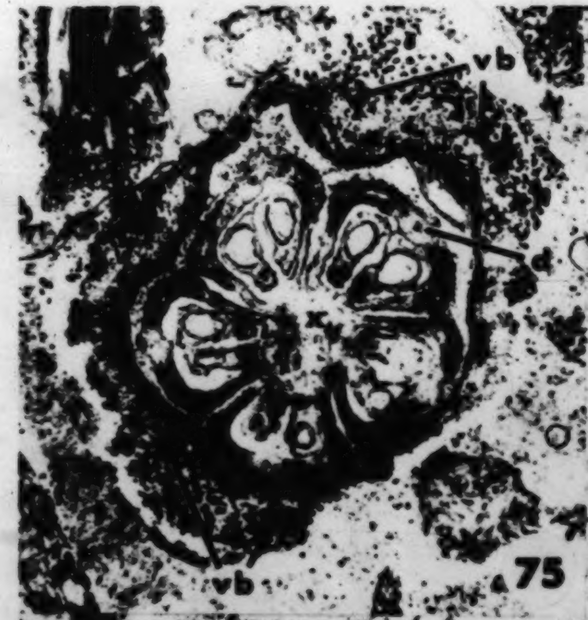
Figs. 75 - 78. Paleorosa similkameenensis. (a = anther; b = bract; c = carpel; d = dorsal vascular bundle; fc = floral cup; p = petal; pd = pedicel; s = sepal; sy = style; vb = vascular bundle in floral cup.)

Fig. 75. Transverse section through the gynoecium showing the floral cup, five carpels, and two ovules per carpel. The obliqueness of the section shows one of the five carpels fused basally with the floral cup. The other four are sectioned above the point of fusion and are seen to be free. Note the vascular bundles of the floral cup. Those opposite carpels supply sepals, those alternating with carpels supply petals. Note also the dorsal bundle in each carpel. P1122 I7 X 41.

Fig. 76. Longitudinal section of a flower in bud stage showing general features. Carpels do not appear in this section, but two styles are evident. Note the bract attached at the base of the pedicel. P1123 B top9 X 38.

Fig. 77. Longitudinal section of a flower in bud stage. The two large anthers were near maturity when permineralized and contain pollen grains. P1118 E bot4 X 31.

Fig. 78. Slightly oblique transverse section through the top of the floral cup showing alternate insertion of petals and sepals. P1122 I9 X 116.



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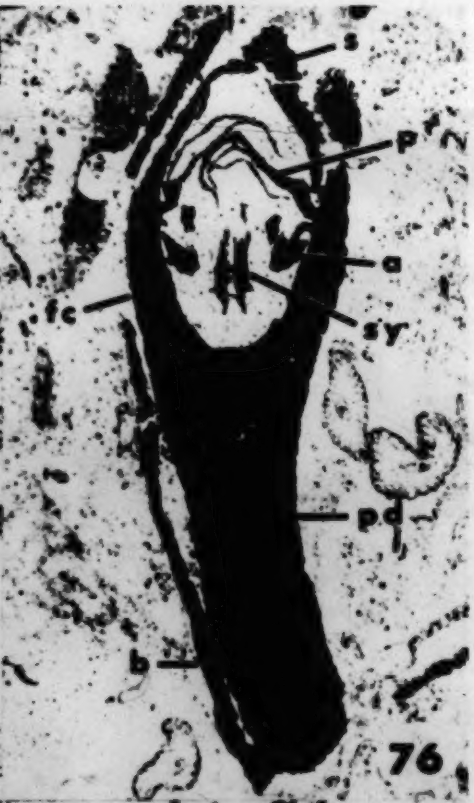
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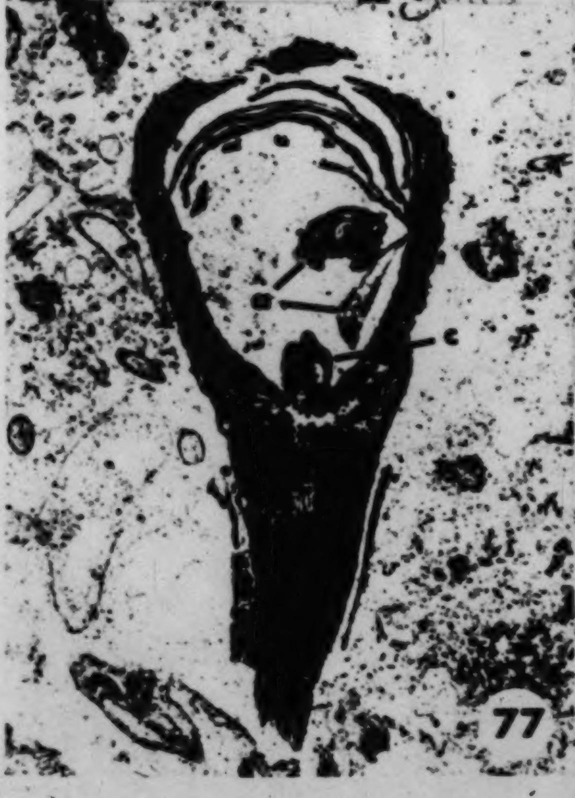

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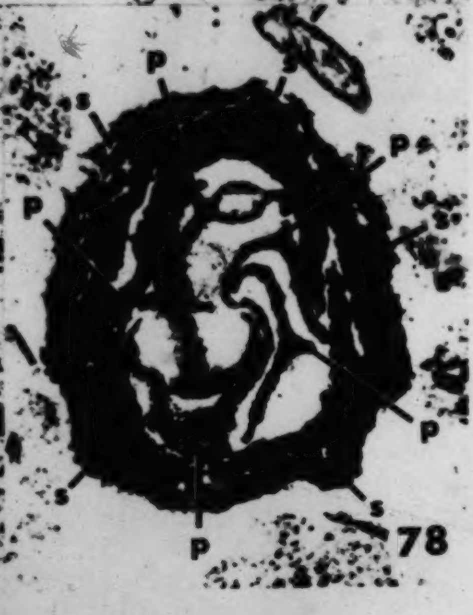
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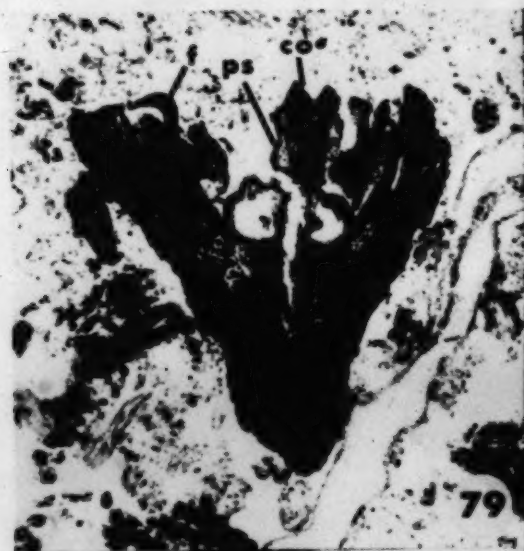
Figs. 79 - 82. *Paleorosa similkameenensis.* (a = anther; co = connective; d = dorsal vascular bundle; f = filament; fu = funiculus; ii = inner integument; oi = outer integument; ps = pollen sac; sy = style; v = ventral vascular bundle; vs = ventral suture.)

Fig. 79. Longitudinal section of a flower showing three anthers. The anther at the center shows the broad connective and attached pollen sacs. The anther at the left shows the dorsal attachment of the filament. P1122 I16 X 35.

Fig. 80. Oblique section showing several anthers in transverse section. Only the connective remains, the pollen sacs having decayed. P1119 J bot8 X 34.

Fig. 81. Oblique section through four carpels showing vasculature of carpels and ovules. Each carpel has two ventral bundles, a dorsal bundle, and a variable number of vegetative bundles. A single bundle is seen in each funiculus. P1143 E bot15 X 38.

Fig. 82. Section similar to that shown in Fig. 81. Inner and outer integuments are indicated. Vasculature as shown in Fig. 81 is also seen here. Note the ventral suture of each carpel. P1143 E bot20 X 52.



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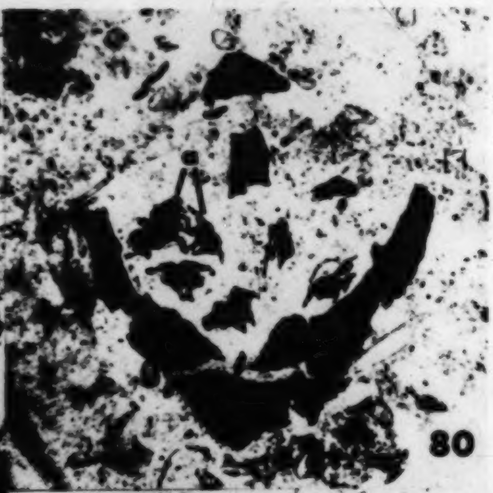

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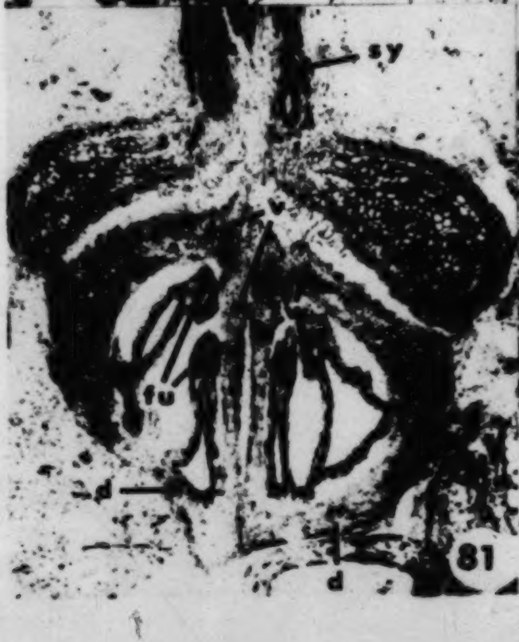

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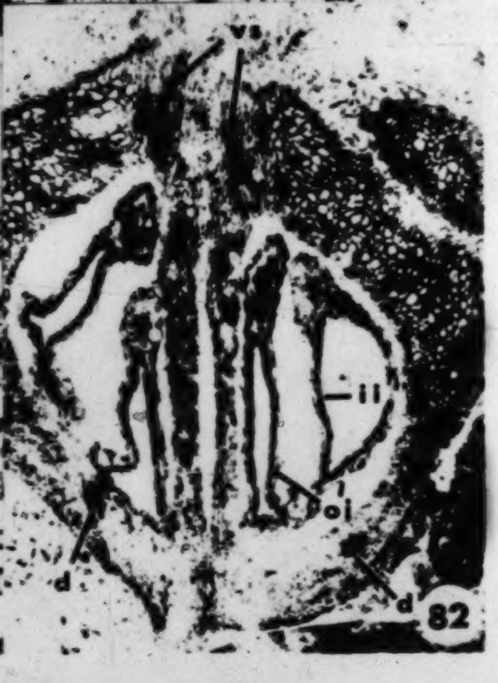

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Figs. 83 - 87. Paleorosa similkameenensis. (a = anther; c = carpel; d = dorsal vascular bundle; fc = floral cup; h = hairs; p = petal; s = sepal; se = septum between adjacent pollen sacs; sy = style; vs = ventral suture.)

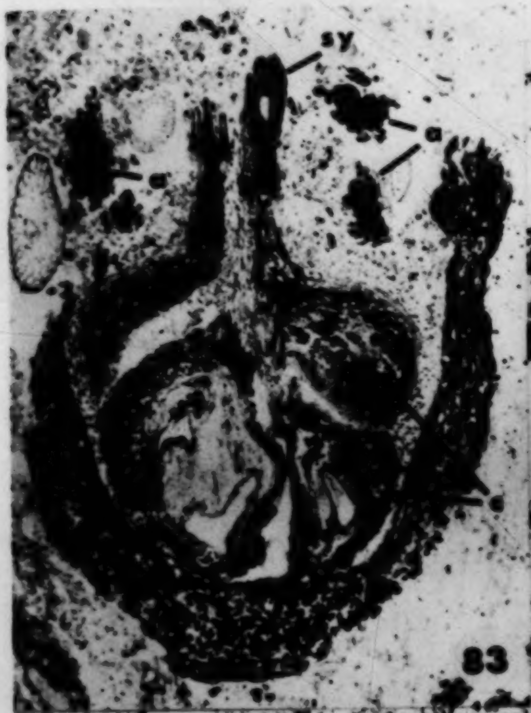
Fig. 83. Oblique section of a flower with well developed carpels in addition to anthers. P1123 L2 19 X 32.

Fig. 84. Longitudinal section of a flower in bud stage showing anthers and carpels. Note the fusion of carpels to the floral cup and the transverse section of the uppermost anther. P1119 J botl X 41.

Fig. 85. Oblique section showing a carpel containing an ovule on the left and the lowest part of the style of a second carpel on the right. Note the hairs covering the surface of both carpel and style. P1143 E botll X 62.

Fig. 86. Oblique transverse section of two styles showing the hollow center, dorsal bundle, and ventral suture. P1122 H bot22 X 120.

Fig. 87. Anthers of the flower in Fig. 77. showing pollen grains. Note the septum which incompletely divides pollen sacs. P1118 E bot4 X 105.



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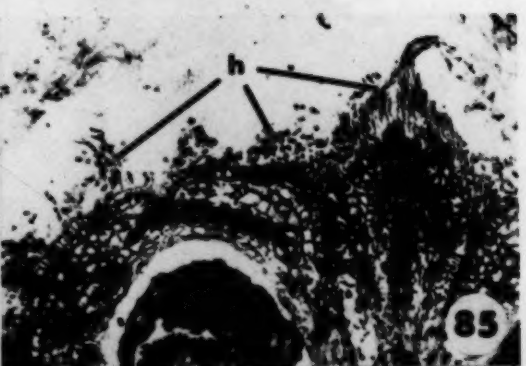

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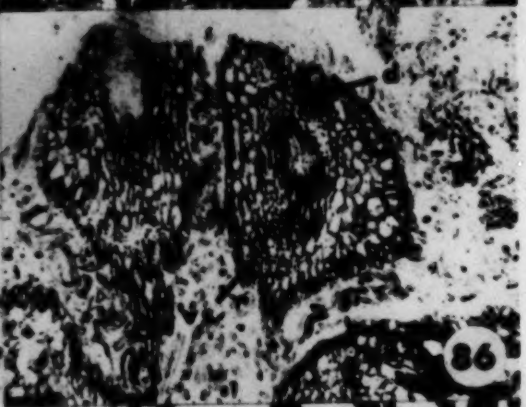

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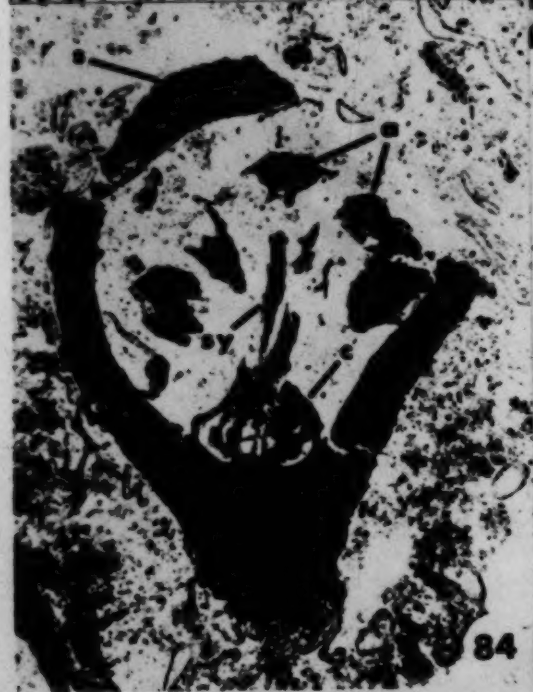

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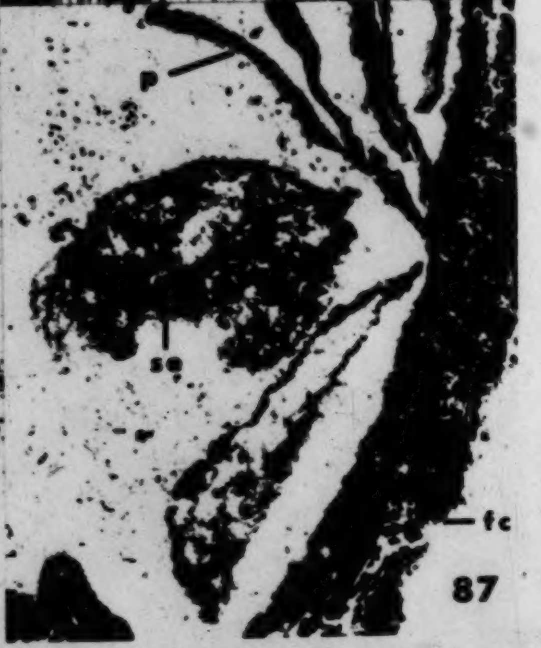


87

Order, Family: Incertae sedis

Eorhiza arnoldii (Figs. 88-98)

DESCRIPTION - Rhizomes and roots of this semiaquatic dicot are found in the majority of chert layers, occasionally in abundance, but usually as a minor component associated with the remains of other angiosperms and Pinus. Leaves and reproductive organs have not been found. Specimens of Eorhiza arnoldii were described in some detail by Robison and Person (1973), but the present study has allowed for minor modification to their description.

Rhizomes are 2 - 3 cm in diameter and somewhat flattened (Fig. 88). That this is the actual shape and not a result of compression is shown by the lack of compaction of cortical aerenchyma and pith cells. The pith is large and solid, with a diameter of about one-half that of the entire rhizome. Surrounding the pith are numerous endarch primary xylem strands (Fig. 91). The secondary xylem is up to 2.0 mm thick and is characterized by vessel elements with oblique, scalariform end walls, scattered parenchyma cells, and both uni- and multiseriate rays (Robison and Person, 1973). The cortex is composed of an inner, aerenchymatous zone and a thin, outer zone of solid parenchyma. The uniseriate epidermis is without hairs.

Although leaves have not been found, remnants of broad, clasping leaf bases are found attached to the rhizomes. They are not restricted to any particular side of the rhizome and appear to be produced in a regular sequence (Fig. 89). The nature of this sequence has not yet been determined. Several very large traces and numerous small ones are found to pass through the cortex and into each leaf base. Leaf trace origin must be studies in more detail before a detailed description can be made. It appears, however, that Eorhiza has multilacunar nodes.

Robison and Person (1973) were unable to determine the nature of lateral branching. They reported the projection of two branch traces into the cortex and the subsequent formation of a vascular cylinder, presumably derived from the two branch traces. As is seen in the series of Figures 93 - 97, branching is quite complex. A large number of traces are given off and assembled to form the lateral branch and a very large branch gap. Leaf traces are produced by the vascular cylinder before the branch has departed. Wherever these departing branches were followed, they were found to form a bud. Enclosing the apex are what appear to be bud scales, for they do not appear to have any kind of a distal, laminar structure (Figs. 97, 98). These branches are borne on the lateral sides of the rhizome.

DISCUSSION - The function of these lateral branches is now open to question. Robison and Person (1973) assumed that their function was similar to that of the main rhizome, or that the formation of these structures was a branching of the rhizomatous system of the plant. Occasionally there are near equal divisions in the rhizomes that resulted in two functional rhizomes. The lateral branches, however, are much smaller than the parent axis and appear quite frequently on the rhizome.

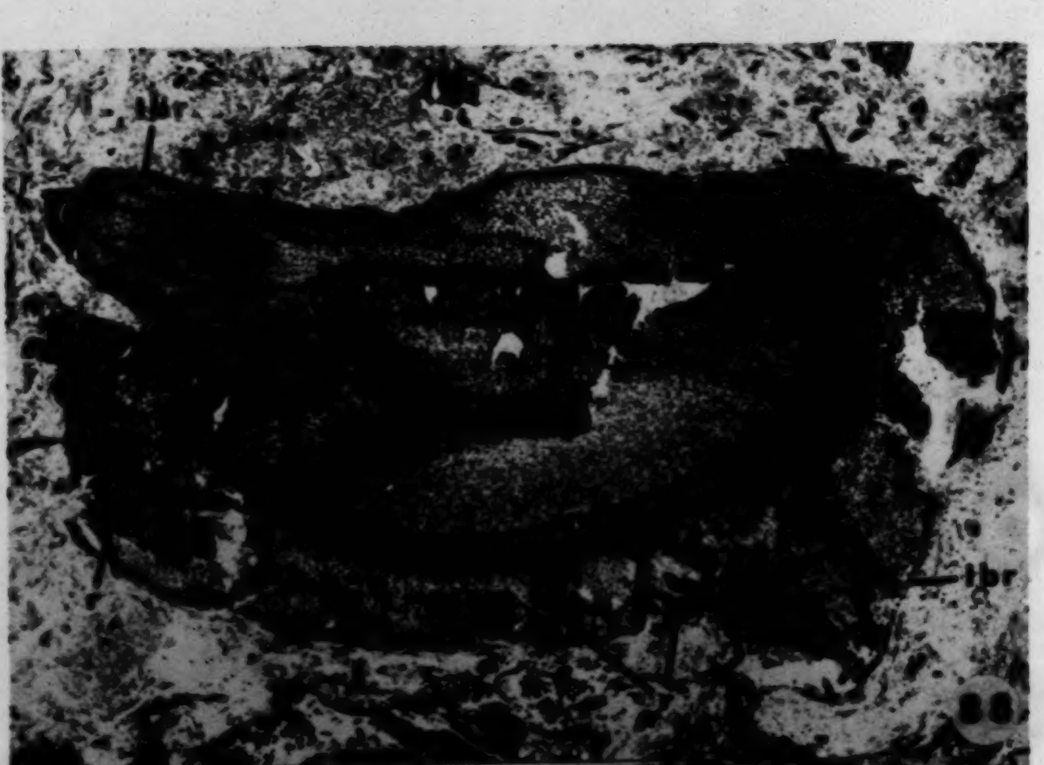
As yet, the only known appendages borne by the rhizomes, are the leaves and the lateral branches. Since Eorhiza must have produced a flowering axis, a suspicion arises as to the function of the lateral branches. It is my belief that these laterals were not destined to become rhizomatous, but that they developed into erect floral axes.

Robison and Person could not determine the taxonomic position of Eorhiza primarily due to the lack of knowledge of the structure of rhizomes of extant plants. Identification of this plant may have to await the discovery of reproductive structures. Numerous seeds and fruits, some of which may have been produced by Eorhiza, are found in association with the rhizome.

Figs. 88 - 89. Eorhiza arnoldii. (lbr = lateral branch; lb = leaf base; r = root).

Fig. 88. Cross section of rhizome showing general features. Note the two lateral branches to the upper left and lower right and the adventitious roots. P1111 D bot8 X 4.3.

Fig. 89. Oblique longitudinal section of a rhizome showing the attachment of several leaf bases. P1143 E bot6 X 5.



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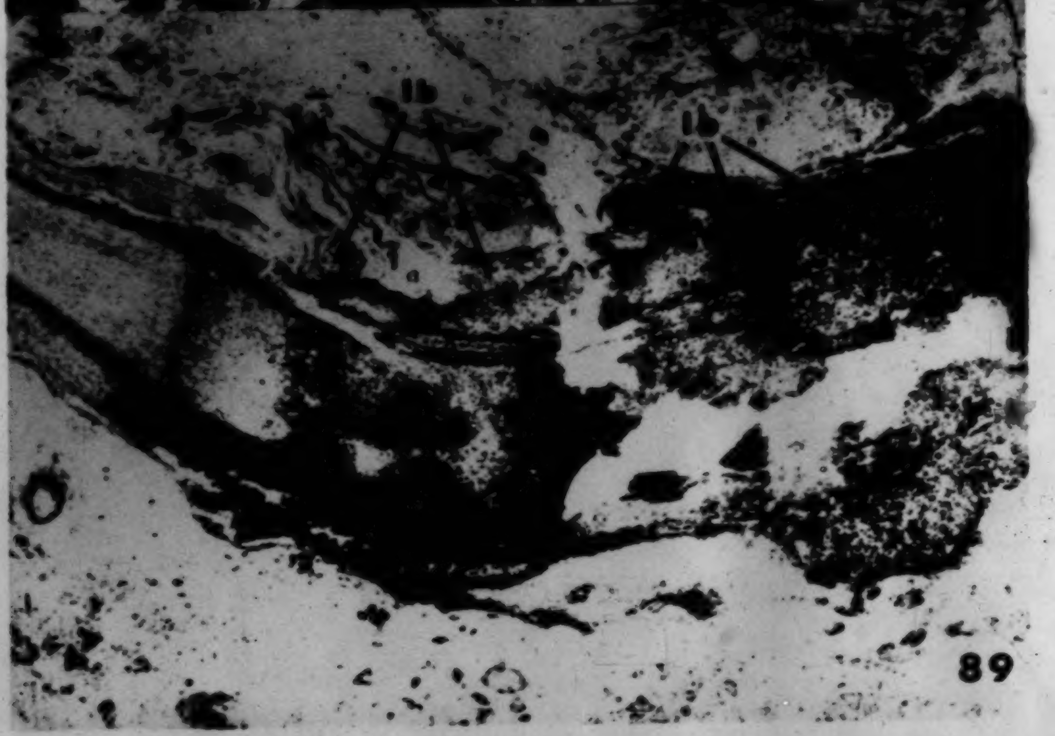


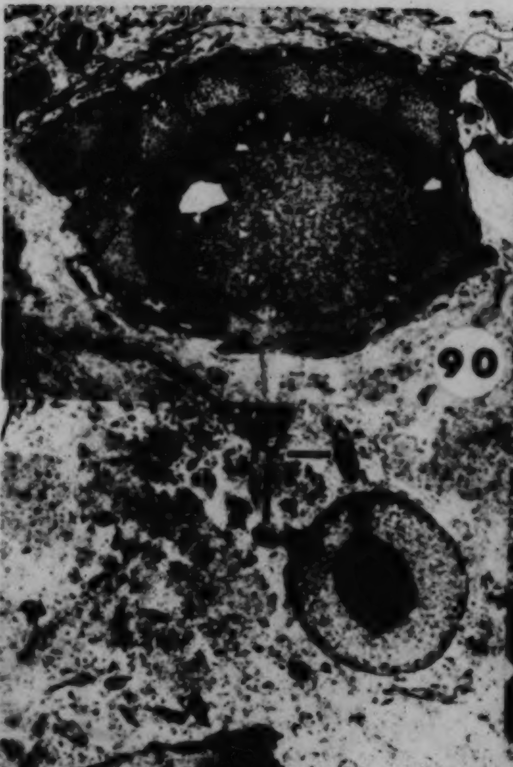
89

Figs. 90 - 92. Eorhiza arnoldii. (lr = lateral root; lt = leaf trace).

Fig. 90. Cross section of a rhizome showing the departure of leaf traces. Note the lateral branch to the upper left. P1111 E top X 3.5.

Fig. 91. Closeup of part of the vascular cylinder of the specimen shown in Fig. 90. Note the leaf traces, solid pith (left), aerenchymatous cortex, and secondary xylem. P1111 E top X 14.

Fig. 92. Cross and longitudinal sections of roots of Eorhiza. Note the aerenchymatous cortex and the production of lateral roots. P1224 B top X 9.



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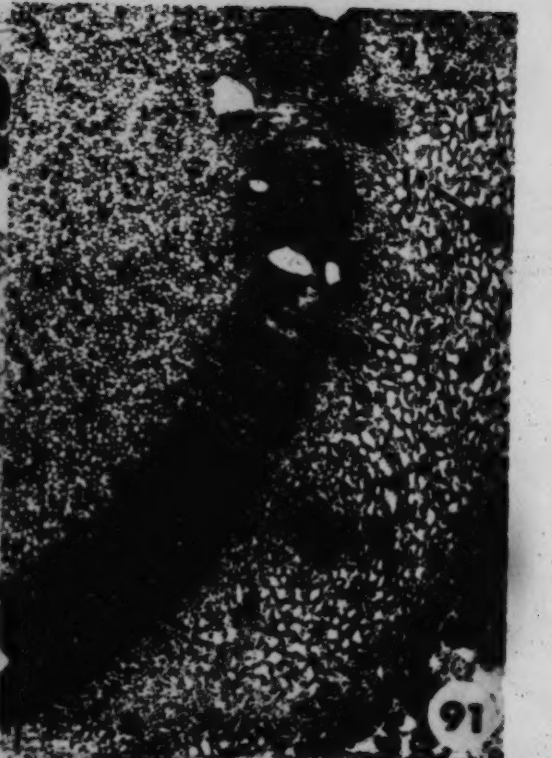

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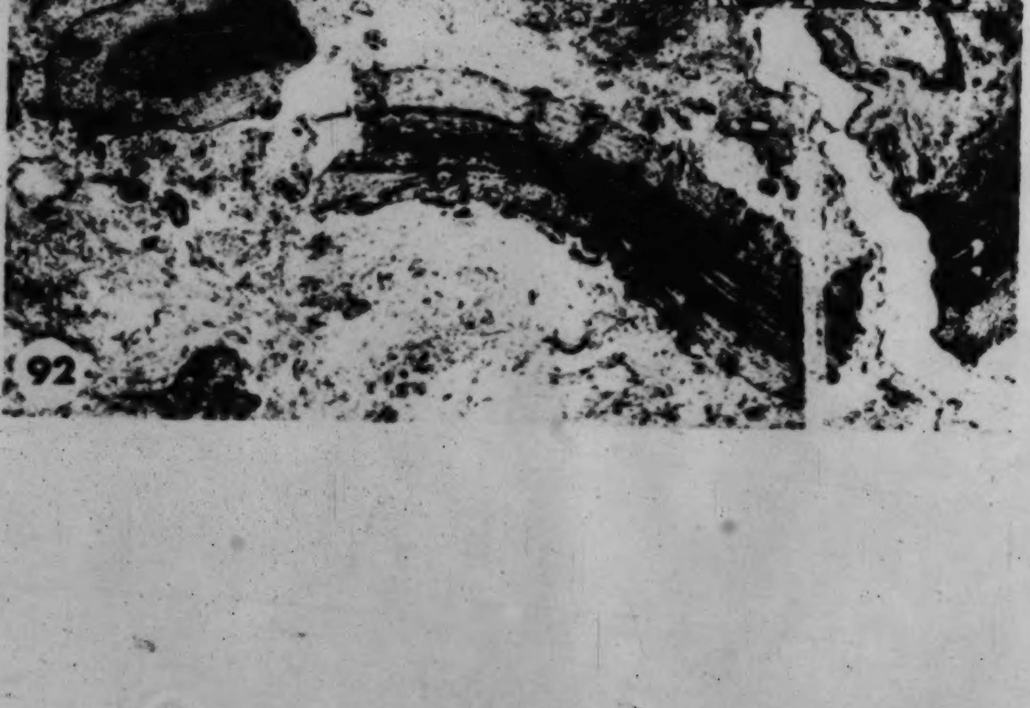

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Figs. 93 - 97. *Eorhiza arnoldii*. Serial cross sections of a rhizome showing the structure of a lateral branch. (bt = branch trace; bg = branch gap; lf = leaf; lt = leaf trace; p = pith; r = root; 2°X = secondary xylem).

Fig. 93. Several branch traces can be seen passing through the cortex of the parent rhizome. Note leaf traces present in the cortex of the lateral branch. The structure left of center is a root. P1111 D bot35 X 6.

Fig. 94. Note the branch gap. P1111 D bot30 X 6.

Fig. 95. Note that interfascicular secondary development has formed a complete vascular cylinder at a short distance from the vascular tissue of the rhizome. P1111 D bot21 X 6.

Fig. 96. P1111 D bot8 X 6.

Fig. 97. Lateral branch with apical scales or young leaves. P1111 D bot1 X 6.

Fig. 98. *Eorhiza arnoldii*. Oblique section of the distal portion of a lateral branch showing their bud-like structure. P1139 C top4 X 10.

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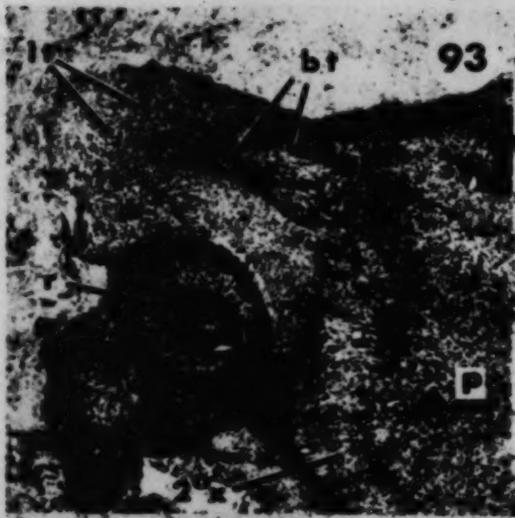
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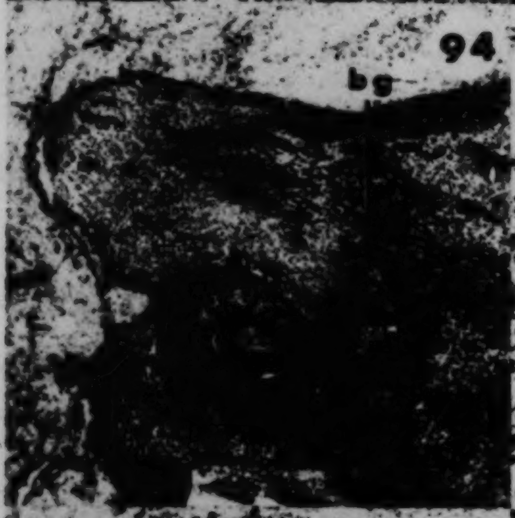
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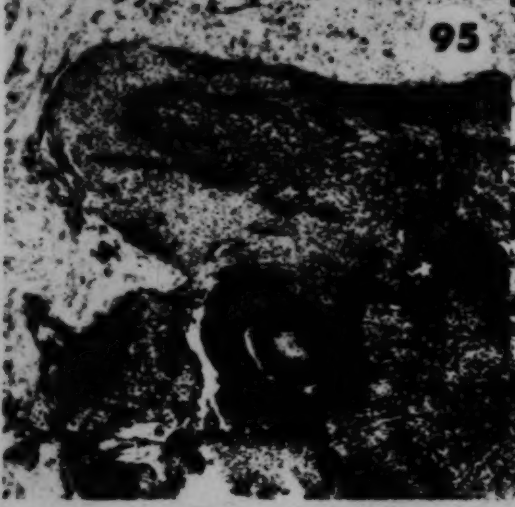
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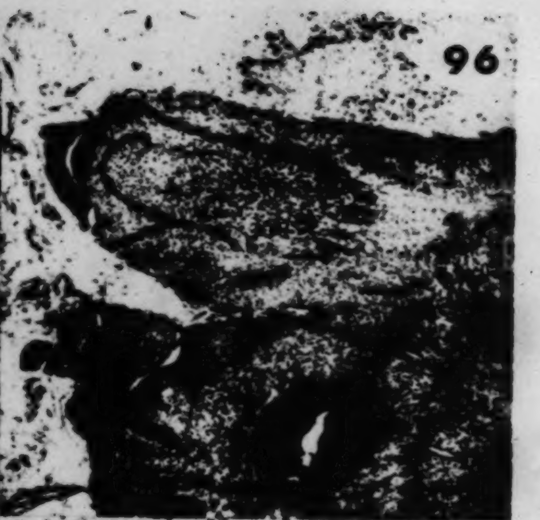
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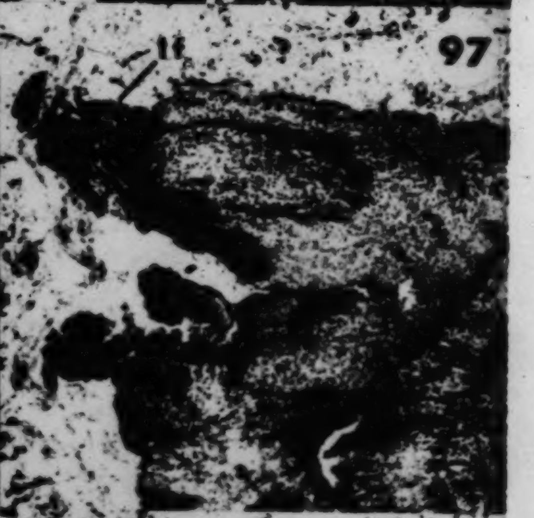
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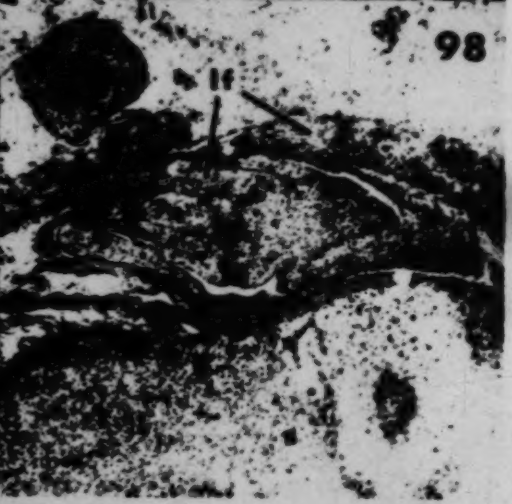
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Incertae sedis

The specimens shown in Figures 99 - 107 have been selected from a large number of as yet unidentified fruits, seeds, and leaf remains. Associated with these organs are several types of dicotyledonous foliage and woody and herbaceous stems. No attempt has yet been made to determine affinities of these plant parts. They will be discussed separately by figure number.

Fig. 99

This fruit is approximately 1 cm in diameter. There are no seeds remaining in any of the five locules, but the large placenta present in each probably bore numerous seeds. This fruit is commonly found in association with Eorhiza arnoldii.

Fig. 100

Numerous seeds are preserved within this fruit. There appears to be four locules, but the septa are not well defined. The dispersed seeds of this type of fruit are perhaps the most common type of seed found in the chert.

Fig. 101

The seeds of this fruit appear to have aborted prior to fossilization, although their structure may be an artifact of preservation. The small seeds of this fruit are about the same size as those of Fig. 100, and are also very common.

Fig. 102

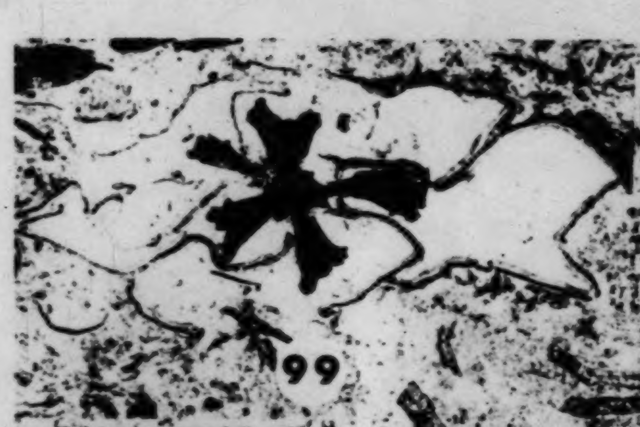
This type of foliage is the most common dicotyledonous foliage present in the chert. An association with any particular reproductive structure has not yet been established.

Figs. 103 - 107

These seeds show good structural preservation of the seed coat, but embryos have not been recognized. In many cases, cellular tissue is found within them, but no structure can be seen. It is possible that this tissue is endosperm.

4

Figs. 99 - 101.	Incertae sedis. Fruits found in the Ashnola chert.
Fig. 99.	Five locular fruit in a post-dispersal state. P1126 G X 6.
Fig. 100.	Four(?) locular fruit containing numerous seeds. P1142 D bot X 14.
Fig. 101.	Fruit with abortive or poorly preserved seeds. P1138 H X 14.
Fig. 102.	Incertae sedis. Dicotyledonous foliage. P1060 F top.
Figs. 103 - 107.	Incertae sedis. Some of the many types of unidentified seeds found in the chert.
Fig. 103.	P1230 D top X 6.
Fig. 104.	P1060 F bot X 10.
Fig. 105.	P1229 D X 11.
Fig. 106.	P1135 C top X 10.
Fig. 107.	1060 G top X 14.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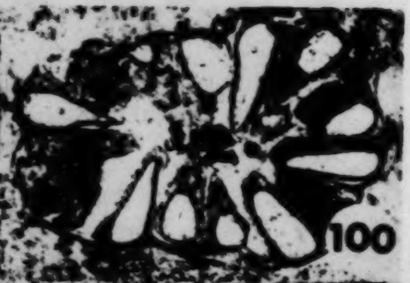
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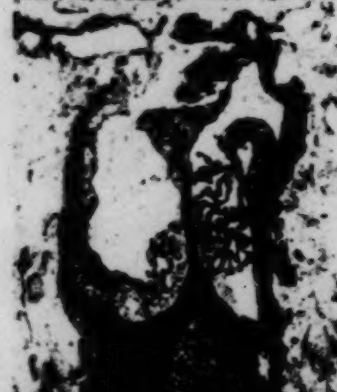
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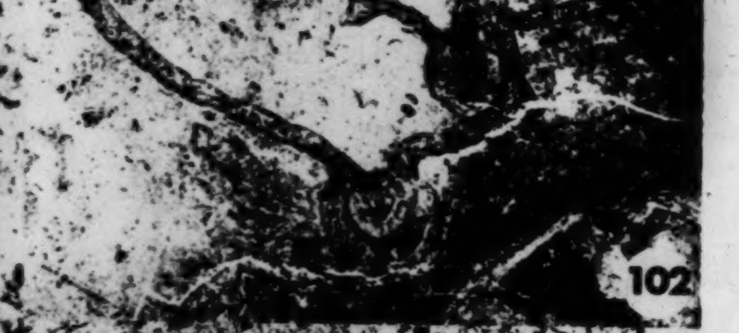
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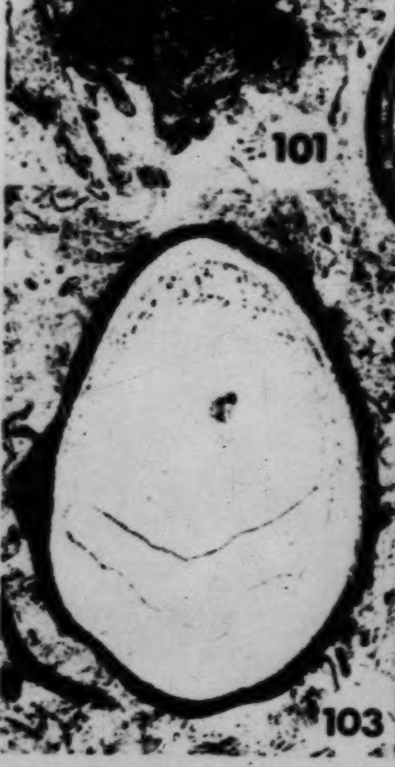
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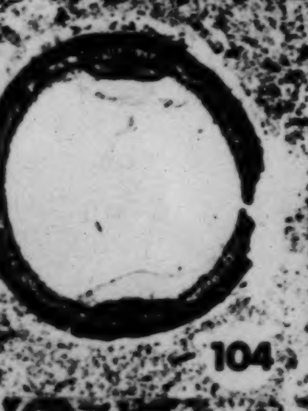
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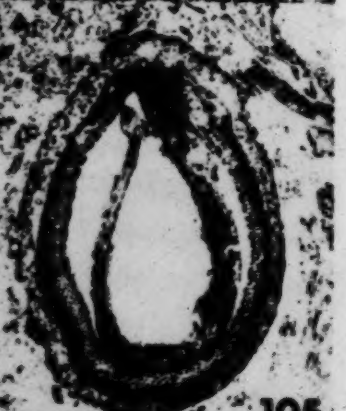
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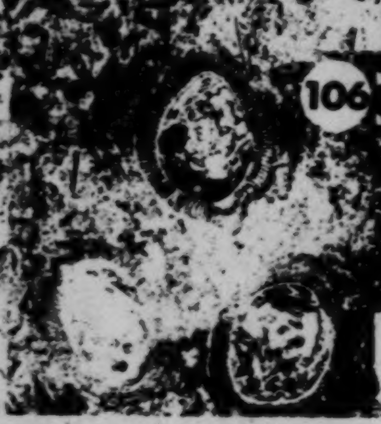
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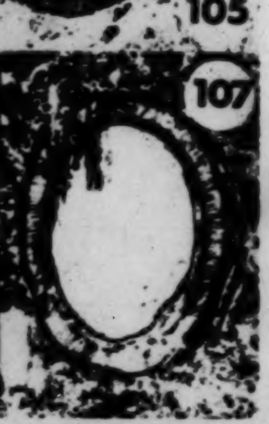

107

Class: Angiospermopsida

Sub-Class: Monocotyledonae

Order: Palmales

Family: Palmae

Incertae sedis (Figs. 108-117)

DESCRIPTION - The remains of petioles, laminae, and roots of this palm are found in abundance in some of the chert layers. No stems or reproductive structures have been identified.

Petioles are 1 - 3 cm in diameter and are somewhat aerenchymatous (Figs. 108, 113). Both vascular and fiber bundles are scattered throughout the ground tissue (Fig. 110). Vascular bundles possess a single, large metaxylem vessel and a number of smaller vessels and tracheids. Phloem is divided into two areas by a zone of fibers. A fibrous bundle sheath encloses the vascular tissue except at points opposite the large vessel.

Midribs and leaf laminae are found in association with the petioles, but have not yet been found attached (Figs. 111, 112). Midribs have more than one (usually three) large vascular bundles at the center and many smaller, fiber bundles at the periphery. The vascular bundles have two to five large vessels, differing from those found in the petioles. A zone of expansion tissue is found between the points of attachment of the lamina.

Roots are found in a wide range of size, but all show the same basic features. The pith of larger roots is generally absent, but is seen to be parenchymatous in smaller roots. A ring of very large metaxylem vessels is found adjacent to the pith (Fig. 114). Trachery element size gradually decreases toward the endodermis, where the numerous protoxylem points can be observed. Cells of the endodermis are thickened on the inner, radial and horizontal walls, while the outer wall is relatively thin. The root cortex is aerenchymatous (Fig. 116), but poor preservation often obscures this.

DISCUSSION - Although these organs have not been found attached, they are in very close association and there appears to be only one type of each organ present. This leads to speculation that they represent a single species. The roots have a structure that appears fairly commonly in palms, but the petioles and especially the midribs are useful in identifying the fossil.

Tomlinson (1961, p. 40) divided the palms into two major groups, among other characteristics, on the basis of midrib anatomy:

> "(i) In the fan-palms of the Sabaloid and Borassoid groups, but not Lepidocaryum and Mauritia of the Lepidocaryoid palms, the central ground parenchyma contains one or more large vascular bundles which are like the large veins of the lamina and, with few exceptions, are not confluent .... . Adaxial and abaxial ribs differ mainly in size.
>
> (ii) In all other palms except Phoenix, i.e. the feather-palms together with Lepidocaryum and Mauritia, there is a complete fibrous cylinder

> occupying most of the rib and enclosing a central colourless ground parenchyma ... . Within this central tissue is a larger abaxial vascular bundle, the phloem of which may be rather diffuse, together with smaller vascular bundles mostly situated adaxially and often inversely orientated, and even isolated phloem strands. These smaller bundles are often embedded in the peripheral fibrous tissue, as in many Lepidocaryoid palms."

The presence of more than one large bundle and the lack of a fibrous cylinder clearly places the fossil in the fan-palms.

An additional characteristic of fan-palms is the presence of a single mass of expansion tissue in the fold of the midrib. In the feather palms, there are two bands of expansion cells, one on each side of the midrib.

A distinction between Sabaloid and Borassoid palms was made by Tomlinson (1961) on the nature of the phloem in the vascular bundles. Borassoid palms have a single mass of phloem in each bundle, while the bundles of Sabaloid palms typically have two phloem zones separated by a fibrous partition. There are two phloem zones found in the vascular bundles of both fossil petioles and midribs. This characteristic is indistinct in Fig. 110 and 112, but in less well preserved specimens the phloem has decayed prior to permineralization and has left behind two cavities separated by the fibrous partition.

On the basis of this evidence, then, the fossil is referred to the Sabaloid palms. More accurate identification must await further study.

This is the first report of palm remains from the

Allenby Formation. The presence of this palm indicates a very warm temperate to subtropical climate in the Princeton area during Allenby time. The aerenchymatous nature of both petioles and roots is reminiscent of the structure of *Dennstaedtiopsis aerenchymata*, unidentified fern B, and *Eorhiza arnoldii* and is further evidence for a marshy habitat at the Ashnola locality at the time of formation of the chert layers.

Fig. 108 - 112. Palmae. Incertae sedis. Petioles and midribs. (bs = fibrous bundle sheaths; et = expansion tissue; fb = fiber bundle; l = leaf lamina, mv = metaxylem vessel; ph = phloem; x = xylem).

Fig. 108. Cross section of palm petiole showing general features. P1124 G bot X 3.

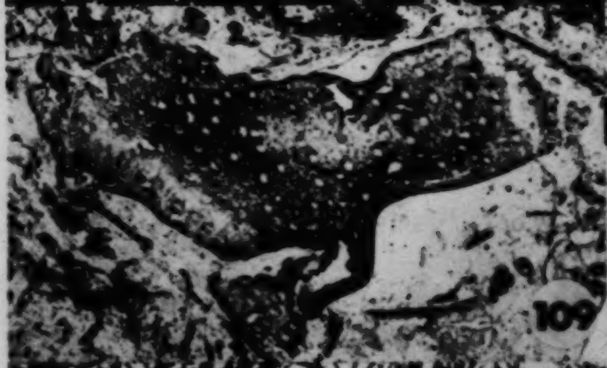
Fig. 109. Cross section of a small petiole.P1171 B bot X 3.5.

Fig. 110. Closeup of vascular bundles and ground tissue of a petiole. The ground tissue is aerenchymatous and contains numerous fiber bundles. The vascular bundles have a single, large metaxylem vessel and several smaller cells of the metaxylem and protoxylem. Phloem is divided into two zones by a band of fibers. The fibrous bundle sheath is discontinuous opposite the metaxylem vessel. Note the tyloses within the vessels. P1165 F2 bot X 71.

Fig. 111. Cross sections of two palm midribs.P1171 C top X 11.

Fig. 112. Closeup of a midrib showing three large, vascular bundles at the center of the midrib and several smaller, fiber bundles at the periphery. Note also the mass of expansion tissue and the remnants of the lamina. P1171 B bot X 68.

108



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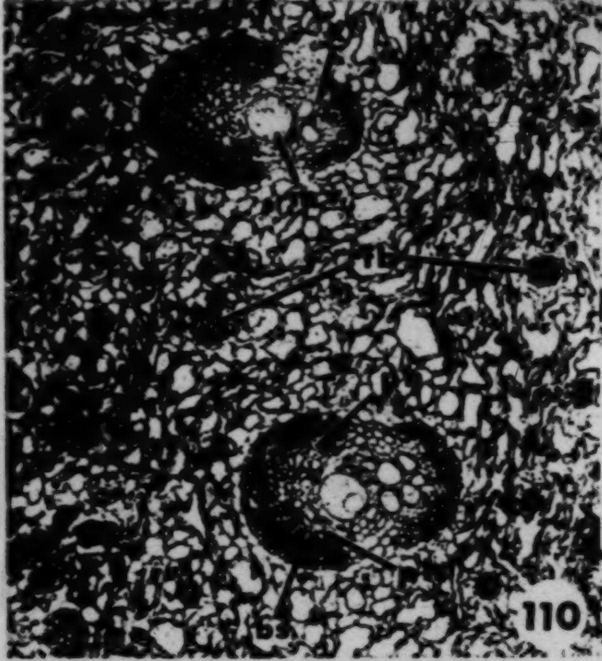

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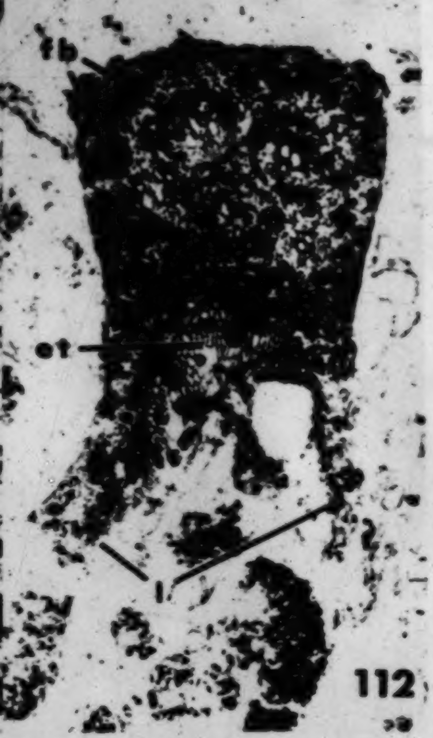

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Fig. 113. Palmae, Incertae sedis. Longitudinal section of a petiole. Note the aerenchymatous ground tissue. P1165 D top X 9.

Figs. 114 - 117. Palmae, Incertae sedis. Roots (lr - lateral root, mv = metaxylem vessel).

Fig. 114. Cross section of a large root. The vascular tissue is composed of a ring of very large vessels interior to smaller vessels and tracheids. A zone of sclerenchyma surrounds the stele. The cortex is primarily aerenchymatous. The pith has not been preserved. P1064 C top X 11.

Fig. 115. Cross section of a large root shown giving rise to a smaller, lateral root. P1165 F2 bot X 6.

Fig. 116. Cross section of a small root showing the aerenchymatous structure of the cortex. P1230 B top X 25.

Fig. 117. Cross section of a very small root. P1171 E top X 44.

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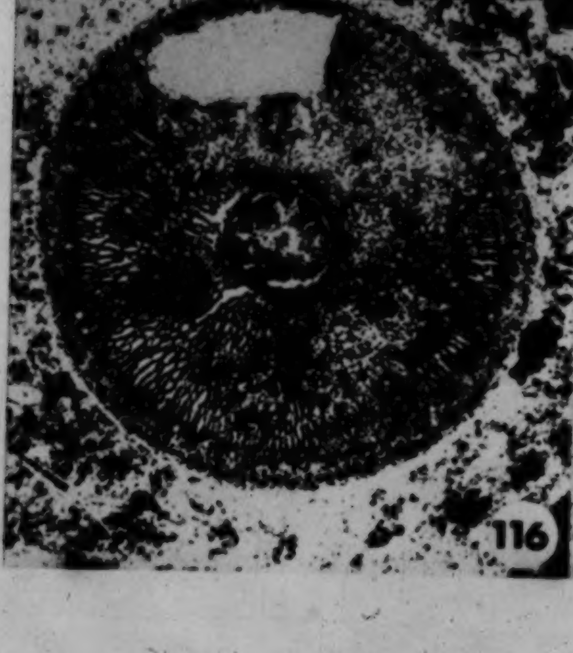
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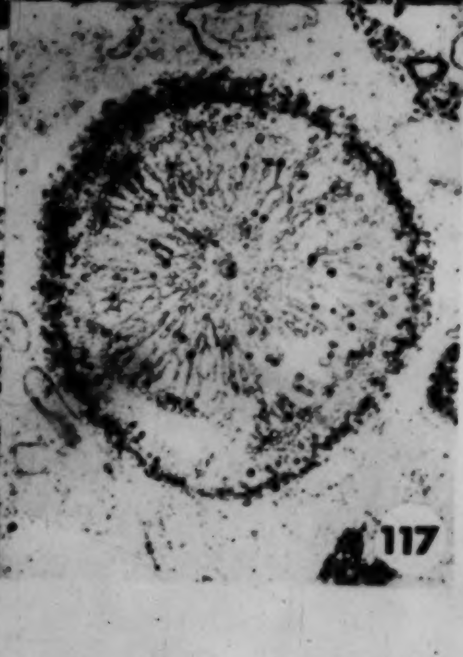
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CHAPTER 5

DISCUSSION

The flora of the Ashnola locality shows an interesting combination of both subtropical and temperate elements. Pinus and Metasequoia indicate a temperate climate. Members of the Maloideae are principally temperate and so, presumably, was Paleorosa. Sabaloid palms, however, are more indicative of a subtropical to very warm temperate environment. In the Clarno Formation of Oregon Dennstaedtiopsis aerenchymata is closely associated with Acrostichum preaureum (Arnold and Daugherty, 1964), the living equivalents of which are found in tropical mangrove swamps. An investigation of climatic conditions present in western North America during the Eocene may help to explain the composition of the Ashnola flora.

Climatic Conditions During the Middle Eocene -

Following a deterioration in world climate at the end of the Cretaceous, there was a warming trend during the Paleocene which reached an optimum during the Eocene. Following this there was again a cooling extending through the Oligocene, a slight recovery during the Miocene, and a rapid deterioration through the late Miocene and the Pliocene which led eventually to the Pleistocene Glaciation (Brooks, 1951). The climatic optimum of the Eocene appears to coincide with the deposition of the Allenby Formation, and at this time floras reached their maximum northern extent.

Although drift of the continents has altered the position of the North Pole relative to North America, latitudinal positions occupied at the present will be retained in discussing the past. This is done because estimations of paleoclimate and paleoecology, as well as correlations of floras and faunas, are discussed in reference to geographical localities which have not changed position relative to one another.

Durham (1950) indicates that the marine clinate at 49° latitude was subtropical to tropical during the Eocene. This warm ocean would contribute to a warm and moist coastal climate. The Ashnola locality now lies in the rain shadow of the Cascade Mountains, but this range was not present during the early Tertiary (Dott and Batten, 1971). Thus, the climate at the Ashnola locality could have been under oceanic influence, although just how much influence could be felt at more than 100 miles from the coast is debatable.

Chaney (1949a) recognizes two distinct types of older Tertiary floras and describes them as follows:

> "The first of these is a subtropical assemblage made up predominantly of broad-leafed evergreen angiosperms whose living equivalents occupy regions in which freezing temperatures are seldom if ever recorded; palms and cycads are represented by a few species which may be abundant; conifers are rare or absent. This forest occupied a zone from California north to Washington on the Pacific Coast, and from New Mexico to Colorado in the interior. Because of its apparent origin in low American latitudes, it is known as the Neotropical-Tertiary Flora. The second major group is a temperate assemblage made up predominantly of broad-leafed deciduous angiosperms, and of conifers both deciduous and evergreen; palms and cycads have not been recorded. This forest

> occupied a zone in Alaska northward beyond the Arctic Circle, extending into the Mackenzie Basin of Canada. Evidence of distribution farther eastward has been destroyed by Pleistocene glaciation, but its former occurrence across northern Canada is suggested by the records of similar plant fossils in the Eocene rocks of Greenland, Spitzbergen, and arctic Siberia. Because of its wide development at high northern latitudes, this assemblage is known as the Arcto-Tertiary Flora. It lived in a region of summer rainfall and winter cold, as judged by the habits of related living trees."

Chaney goes on to say that oceanic influence allowed some of the southern forms to exist on the Pacific coast as far north as Alaska. Inland, however, typical Arcto-Tertiary forms would be found. Although the concept of Neotropical- and Arcto-Tertiary geofloras has met with well-founded opposition (Wolfe, 1969), a diminuition of the tropical elements northward would be expected to have occurred in the Eocene in a similar way as occurs at present.

The Ashnola locality is located in an area which may be considered transitional. It is far enough inland that the ameliorative effect of the ocean would be somewhat reduced, but probably not far enough north to be subject to severe frost. Of this transitional zone Chaney (1949a) says:

> "In the areas between these two major zones of vegetation there is a record of a forest made up of largely temperate trees. Living with them were several members of the subtropical forest which appear to have made their way northward beyond the range of occurrence of most of their associates, during the relatively mild days of the early Tertiary. This ecotone is best developed in southeastern Alaska, on Kupreanof Island at latitude 56 to 57 degrees north. Here is the typical Kenai flora, as described by Hollick (1936) from 55 localities in Alaska, including such temperate trees as redwood

> (Metasequoia), katsura (Cercidiphyllum), birch (Betula), alder (Alnus), hazel (Corylus), hornbeam (Carpinus), chestnut (Castanea), oak (Quercus) and elm (Ulmus). Immediately associated, and often on the same slabs of rock, are the leaf impressions of several members of the Neotropical-Tertiary Flora; these include two genera of cycads (Dioon and Ceratozamia), a fan palm (Flabellaria), laurels of the avocada (Persea) and lance-wood (Ocotea) type, magnolia (Magnolia) and catmon (Dillenia)."

Chaney (1949a) describes this zone as extending along the northern Pacific coast and stretching eastward from southern British Columbia to southern Saskatchewan, and to Montana and North Dakota. The flora of the Ashnola locality, which is contained within this transitional zone, coincides with the proposed vegetation and climate of the region.

Altitudinal Effects on Vegetation in the Princeton Area During the Middle Eocene -

In addition to latitude having an effect upon vegetation, it is also expected that altitude should bring about a response in floral composition (Chaney, 1949a; Axelrod, 1966). Axelrod (1966) gives an estimation of 750 meters for the elevation of the Princeton area during the Eocene, but does not give his basis for such a value. He likely followed Rouse (1962) who believed that the relationships between the Burrard and Allenby floras indicate a similar altitudinal difference as exists today.

Uplift of part of the Cordillera including the Princeton area during the formation of the Rocky Mountains is believed to have been responsible for the severe erosion of the Paleozoic rocks of the area (Dott and Batten, 1971).

It was previously noted that local subsidence during the Eocene most probably initiated deposition in the vicinity of Princeton. It is conceivable, then, that much of south central British Columbia could have had an elevation close to that proposed by Rouse and Axelrod. The basins formed by subsidence were possibly much lower than the surrounding hills, for they are filled with great thicknesses (2500 meters at Princeton) of basically coarse sediments and volcanics.

Although the elevation of the Ashnola locality could not have posed hardships on the vegetation, for palms are abundant, different floral assemblages may have existed at higher altitudes in other parts of the Princeton basin and contributed to misinterpretations of the age of the sediments.

Comparison of the Ashnola Locality with Other Localities of the Allenby Formation -

A great deal of difficulty exists in comparing permineralized with compressed plants. While leaves are the most common and easily recognized element in a compression flora, they are of very little use in a permineralized state, where laminar shape is almost impossible to determine. Likewise, anatomical detail of woods and reproductive organs, which is so important in a permineralization flora, is not applicable to compressed plants.

Since evidence for specific comparisons of plants of the Ashnola chert with other localities is, therefore, lacking, only very general comparisons are possible.

(For lists of fossil plants from the Allenby Formation, see Dawson, 1890; Penhallow, 1908; Arnold, 1955). Some of the Ashnola plants such as *Eorhiza*, palms, and ferns have not been reported from other localities of the basin, but this may be due to the unusual conditions of fossilization at the Ashnola locality. Both *Metasequoia* and *Pinus* are found in other localities (Arnold, 1955). Miller (1973) attempted to link *Pinus similkameenensis* with *P. latahensis* of *P. tulameenensis*, two five-needle pines from the Allenby Formation, but found differences in size too great. Dicotyledonous remains have yet to be dealt with. Distinct growth rings found in the various types of ring-porous woods indicate a winter dormancy that was probably accompanied by a deciduous habit, although growth rings may be produced by drying as well as cold. Forests represented by other localities are basically deciduous.

The temperate aspect of the Ashnola flora appears similar to other floras of the Allenby Formation, although evidence is yet incomplete. A major difference is in the presence of more tropical elements at Ashnola, for this is the first report of palms in the Princeton area. I believe that these palms are an indicator of a rather mild climate in the area, but they could be the result of an unique microclimate possibly created by the warm mineral springs responsible for periodic permineralization. It is possible that the palms were able to withstand cool temperatures and do not signify a warm climate. However, in consideration of the ranges of modern palms and the nature of the plants associated with fossil palms, this is unlikely. It is the temperate aspect of the composite flora, which was compared with temperate floras typical of late Tertiary deposits, of the Allenby Formation that has resulted in misinterpretations of the age of these sediments.

Discrepancies in Age Determinations of the Allenby Formation -

Megafossil evidence led early investigators to believe that the Allenby Formation was of late Tertiary age (see Ashnola Locality - Age). Some recent work tends to support this as well (Chandrasekharam, 1975). In light of an established Middle Eocene age for the deposits, reasons for these contradictory determinations have been sought:

1) The inclusion of younger fossils in collections - An unconformity within the Allenby Formation would allow for the presence of younger material which could affect interpretations. Although no unconformities have been recognized within the Allenby Formation (Hills, 1965a), late Tertiary fossiliferous sediments that overlay part of the Princeton basin have been recognized by Mathews and Rouse (1963). If fossils from these deposits were included in early collections, as Mathews and Rouse suggest, confusion would result. However, localities exploited by the early investigators were primarily in the southern and western portions of the basin, while late Tertiary deposits were found only in the northern and eastern areas. In my opinion it is unlikely that a significant number of fossils from the younger

sediments would have been included in the early collections.

The relationships of the locality being worked on by Chandrasekharam (1975) to the Allenby Formation is still in question. The material is most certainly late Miocene, but is unlike other collections from the Allenby Formation. The material is found at the northern limits of the basin and is apparently quite high in the sequence. The nearby hills are capped by late Tertiary deposits, and it is my belief that this material has slumped from the late Tertiary beds and is now being confused with the older Tertiary sediments of the Allenby Formation.

2) The misinterpretation of floral assemblages - If it is assumed that younger material did not accompany early collections, a misinterpretation of the data is the cause of the conflicting ages. The introduction of temperate forms such as Pinus, Picea, Abies, Acer, and Betula (Arnold, 1955) could have been caused by:

a) The occurrence of brief climatic deterioration during the Eocene, which has been proposed by Brooks (1951), could have changed the aspect of the flora during Allenby time (Rouse, 1962). Hills (1965b) and Boneham (1968) found palynological evidence for zonation within the Allenby Formation. Boneham (1968, p. 34) suggests that:

> "It is possible that in the sediments below the Princeton-Black Seam the subtropical components of the flora are greater than above the Princeton-Black Seam. If such is the case, and it is not possible to say at this time due to a lack of data, then the Allenby Formation contains a record of changing climates which is worth further investigation."

Whether this apparent zonation is due to a climatic change or to some other physical change in the environment in the basin is open to question. The Ashnola locality is 600 meters above the Princeton-Black Seam and has at least one subtropical element, a sabaloid palm, which is very abundant.

b) The presence of a combination of subtropical to temperate forms, as is well shown by the Ashnola locality, could be a result of the mixing of northern and southern floras in a transitional zone.

c) Plant parts from floral assemblages at high altitudes could have been transported into the basin and then influence assemblages at various localities in the basin.

Some of the early age determinations were taken from comparisons of the Allenby flora with floras of other presumed late Tertiary formations which have since proved to be much older. Bell (in Rice, 1947) found similarities between the Allenby and Kitsilano floras, both of which he believed to be Oligocene. Arnold (1955) felt that the Allenby flora resembled the Republic flora, which he believed Oligocene. Since that time, the Kitsilano Formation has been found to be Middle Eocene (Rouse, 1962) and the Republic, latest Paleocene (Axelrod, 1966). Indeed, our understanding of Cretaceous and Tertiary floras has undergone a dramatic change with new approaches to the identification and interpretation of particularly angiosperm fossil remains (Hickey, 1973; Dilcher, 1974). The cool temperate forms present in the Allenby flora have misled investigators in the past into believing in a later Tertiary age. However, I expect that a thorough reinvestigation will reveal a definitely early Tertiary, although somewhat temperate, assemblage.

Summary of Environmental Conditions at the Ashnola Locality During the Middle Eocene -

The Ashnola locality was described as the remains of an ancient marsh or bog of limited extent (see Ashnola Locality - Formation). Many plant organs have been preserved _in situ_ (_Dennstaedtiopsis_, _Eorhiza_, palms) and show adaptations to an aquatic or semiaquatic habitat (aerenchyma).

If an observer were present at the Ashnola locality during the Middle Eocene, he would probably find himself in a small marsh, perhaps no larger than a few acres, on a valley floor. The water of the marsh would not be deep, and most of the area would be covered by hummocky vegetation including _Dennstaedtiopsis aerenchymata_ and _Eorhiza arnoldii_. Immediately surrounding the marsh would be a dense forest of _Metasequoia_, _Pinus_, and fan palms. The undergrowth would include ferns and _Paleorosa similkameenensis_. The forest of the surrounding hills may have had a more conspicuous deciduous element and palms would be absent. The climate, which could be termed subtropical to warm temperate, would be quite warm and moist, with winter frost rare or absent.

Future Possibilities of the Ashnola Locality -

The plants described in this thesis are a selection of the best known representative forms found in the Ashnola chert. Thus, the actual diversity of the flora is much greater than has been presented here. Among Tertiary permineralization localities, this diversity is rivaled only by that found at Mohgaon Kalan in the Deccan Intertrappean Series of India. However, the plants found at Mohgaon Kalan and at Ashnola are not similar. Few specimens have been reported from other Tertiary permineralization localities.

The Ashnola locality, then, presents an opportunity to study early Tertiary plant structure and reproductive mechanisms in a way not previously possible in North America. This thesis has served to reveal the diversity of the Ashnola flora and to provide a detailed description on a single member of the flora, _Paleorosa_ _similkameenensis_. Many other plants, including _Metasequoia_, palms, ferns, and the numerous dicotyledons, await study. _Paleorosa_, _Pinus arnoldii_, and _Pinus_ _similkameenensis_, which are the only well-described plants from the chert, have already provided valuable information on evolution within the Rosaceae and Pinaceae. It is quite possible, then, that an investigation of other forms will provide similar insights into evolution within other groups. In view of the great potential of the Ashnola locality, continued research on this material should be considered as high priority in the field of Cenozoic plant development and evolution.

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